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TULANE STUDIES IN ZOOLOGY AND BOTANY

VOLUME 23
1980-1981

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY AND BOTANY, a publication of the Biology Department of Tulane University, is devoted primarily to the biology of the waters and adjacent land areas of the Gulf of Mexico and the Caribbean Sea, but manuscripts on areas outside this geographic area will be considered. Each number contains an individual monographic study or several minor studies. Normally two numbers plus an index and a table of contents are issued annually. Preferred citation of the journal is *Tulane Stud. Zool. and Bot.*

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Copies of *Tulane Studies in Zoology and Botany* sent to regular recipients, if lost in the mails, will be replaced if the editorial offices are notified before the second subsequent issue is released.

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ISSN 0082-6782

TULANE STUDIES IN ZOOLOGY AND BOTANY

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HARVARD UNIVERSITY

Volume 22, Number 1 $4.00 May 26, 1980

THE *SHREVEI* GROUP OF HISPANIOLAN *SPHAERODACTYLUS* (REPTILIA, GEKKONIDAE)

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THE *SHREVEI* GROUP OF HISPANIOLAN *SPHAERODACTYLUS* (REPTILIA, GEKKONIDAE)

ALBERT SCHWARTZ and EUGENE D. GRAHAM, JR.
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ABSTRACT

The Hispaniolan *shrevei* group of *Sphaerodactylus* is composed of four species, one of which (*S. asterulus*) is described in the present paper. Detailed descriptions of the four included species are presented, as well as a hypothetical history of the group. *S. shrevei* stands alone, whereas the other species show an interrelationship in pattern. The group is considered to be not closely related to other Hispaniolan or Antillean *Sphaerodactylus* and to be north island (*sensu* Williams) in affinities.

On the Antillean island of Hispaniola occurs a group of species of *Sphaerodactylus* without obvious close relatives there or elsewhere in the West Indies. The first-named of this group of lizards is *S. shrevei* Lazell, and the group-name is derived from this species. Two other species have been described: *S. rhabdotus* Schwartz and *S. leucaster* Schwartz. The latter two species were named on limited material; there was only the single female holotype of *S. shrevei*. *Sphaerodactylus rhabdotus* and *S. leucaster* have complementary distributions in the Dominican Valle de Neiba and the contiguous Llanos de Azua to the east, and *S. leucaster* extends northward toward the Valle de San Juan. *Sphaerodactylus shrevei*, on the other hand, was described from the Haitian Presqu'île du Nord Ouest, at Môle St. Nicholas, removed some 250 km airline from the nearest records for *S. rhabdotus*. We have re-examined the holotype (formerly lost but now found) in light of six new specimens. Small primary series of *S. leucaster* and *S. rhabdotus* have gradually been amplified with additional specimens (rarely series), so that we now know more about the variation in these two species than we did previously.

One problem in obtaining examples of this group of sphaerodactyls is that they are xerophiles, inhabiting rigorous and often hazardous terrain -- cactus and *Acacia* forest -- where collecting is difficult. Other than the very large series of the new species described herein, most of which was native-collected, the senior author secured only one specimen from native collectors. The edificarian situations that allowed the collection of the original lots of *S. leucaster* and *S. rhabdotus* no longer exist. Search for these two species of geckos in non-edificarian situations under fallen and decayed arborescent cactus trunks, in decayed *Acacia* trunks, both prostrate and standing, in palm litter, and under rocks, as well as under and in the dead basal rosettes of *Agave* leaves has yielded occasional specimens. This labor has resulted in the accumulation of

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19 specimens of *S. leucaster* and 27 of *S. rhabdotus*. The largest single series of either species is 15 specimens of *S. rhabdotus* from the type-locality, with nine specimens of the same species collected by James R. Dixon near La Descubierta. The series of eight specimens of *S. rhabdotus* from the type-locality is the largest series of that species; all other localities are represented by one or two specimens.

We emphasize the above for a particular reason. In August 1977, we had brought to us, with many specimens of *S. cinereus* Wagler, at Terre Sonnain, north of Les Poteaux, a single specimen of a gecko that obviously belonged to the *shrevei* group. The lizard was in poor condition. It seemed likely that we were at the periphery of its range, since among many lizards, this one specimen was brought to us. Another possibility was that the native collectors there were collecting in a fashion that did not encourage the taking of this type of gecko. Since *S. cinereus* is primarily edificarian or arboreal (under the loose bark of trees), it is conceivable that the local Haitians were concentrating their efforts in such situations and were not looking under groundcover as a general collecting procedure. On 20 June 1978, we traveled the coastal road between Gonaïves and Coridon for a few kilometers west of Ça Soleil. This trip, west of the Terre Sonnain locality, was an effort to locate more individuals of the same species.

We stopped at an uninhabited locality 9.3 km W Ça Soleil (Fig. 3). The road at this point passes through a series of limestone hills with cliffs, many loose rocks, boulders, and other debris; the most conspicuous plant is *Agave*, of which there were not only large living plants but many decaying basal rosettes of leaves of plants long dead. In addition, there were small piles of rocks scattered over a relatively level area between two hills. Everything seemed to be appropriate for finding some sort of xerophilic gecko. We had success almost immediately and secured a series of 42 lizards in about 45 minutes by searching in the rock piles and in the *Agave* rosettes; five unhatched eggs (and many empty shells) were also found. The series of lizards agreed with our single specimen from Terre Sonnain from the previous summer. Most amazingly, this species appeared to be locally extremely abundant in contrast to all other members of the group.

As we traveled beyond this locality, we encountered a few roadside huts as well as a small village whose name, after that of this entire region, is Lapierre. Inhabitants of this village were avid collectors and obtained an immense series for us. We later proceeded across the limestone hills to a sea level oasis, where this gecko was also abundant (although it occurred there with two other species, one similar to *S. altavelensis* Noble and Hassler and the other undescribed). We have only one record from farther along (15.7 km W Ça Soleil) the road to Coridon, but we feel certain that its distribution continues still farther along the very xeric and very sparsely inhabited coast. At the town of Coridon, we were unsuccessful in securing specimens but feel that this was due to the abundance there of the much more easily secured *Ameiva chrysolaema* Cope - the only lizard brought to us by the local inhabitants.

Considering the proximity of the Lapierre area to the type-locality of *S. shrevei* (80 km airline) and its distance from the nearest record of *S. rhabdotus* (130 km airline), we were struck by the similarity in coloration and pattern of these new lizards to *S. rhabdotus* and *S. leucaster*, and not to *S. shrevei*. Basically, *S. shrevei* is blotched, whereas *S. leucaster* and *S. rhabdotus* are longitudinally striped or lined. The new geckos agree with the lat-

ter pair, most especially with *S. leucaster* in that the longitudinal lines are interrupted by tiny white dots. These dots are much smaller than are the similar white blotches or "stars" that interrupt the longitudinal lines in *S. leucaster*. We accumulated a series of 448 specimens of the new species from the Lapierre region. With this huge lot of specimens, as well as the more abundant material of both *S. leucaster* and *S. rhabdotus*, this seems an appropriate time to review this group of xerophilic geckos.

The *shrevei* group may be characterized by the following combination of characters: 1) size moderate; maximum size 31 mm snout-vent length in males, 32 mm in females; 2) dorsal scales large, keeled, subimbricate to not imbricate, and with or without a few scattered middorsal smaller scales forming an incomplete middorsal zone; 3) dorsal scales with

dorsal smaller scales forming an incomplete middorsal zone; 3) dorsal scales with

hair-bearing scale organs only; 4) throat, chest, and ventral scales smooth; 5) internasal scales usually 2; 6) supralabial scales to mid-eye usually 4; 7) escutcheon extremely variable within species, from 1 to 9 scales in length and from 6 to 25 scales in width, maximally extending to behind the knees laterally; 8) sexual dichromatism weak to absent in basic pattern, but coloration of head different in males and females; 9) dorsal pattern either lineate or blotched, head in males yellow to orange, no dark head pattern present; 10) no scapular patch and included ocelli; 11) ontogenetic variation in dorsal pattern apparently absent; 12) head short and blunt, with a convex snout; 13) pupil of eye vertically elliptical rather than circular.

TAXONOMIC ACCOUNTS

Sphaerodactylus shrevei Lazell

Sphaerodactylus shrevei Lazell, 1961, Breviora (139):1.

Type-locality: Môle St. Nicholas, Département du Nord Ouest, Haiti.

Holotype: MCZ 62548.

Definition. An Hispaniolan species of *Sphaerodactylus* characterized by the combination of: 1) dorsal scales subimbricate or not imbricate, with an ill defined middorsal zone of smaller keeled scales not forming a continuous dorsal row; 2) high number of scales (38-46) around midbody; 3) modally 1 internasal scale; 4) dorsal pattern basically blotched and not lineate, with about 5, more or less symmetrical, pairs of blotches on each side of the dorsal midline (Fig. 2); 5) an irregular ventrolateral line of much smaller blotch-like figures.

Description. There are now seven specimens of *S. shrevei*: the holotypic female, three adult females, one subadult male, and 2 juveniles (snout-vent lengths 14 and 17 mm). Scale counts and measurements for the series are: largest male (ASFS V49555) with a snout-vent length of 24 mm, largest females (MCZ 62548, ASFS V49769, ASFS V49831) 30 mm; dorsal scales between axilla and groin 22-27 ($\bar{x} = 23.8$); ventral scales between axilla and groin 31-33 (32.2); midbody scales 38-46 (42.0); supralabials to mid-eye modally 4/4 (five individuals) but two individuals have counts of 5/5; internasal modally 1 (5 individuals), but two specimens have 2 internasals; fourth toe lamellae 10-11 (10.3; $M_O = 10 - 75\%$); escutcheon in single male 6 X 25, consisting of a central group of thickened scales with a single row of scales extending to behind the knee. Lazell's description of the holotype agrees well with the condition in the fresh material. *Sphaerodactylus shrevei* is a blotched (rather than lineate) lizard. There is a broad dark gray cephalic U enclosing a darkly stippled snout, followed by a supraaxillary pair and a postaxillary pair of more or less rectangular

dark blotches; these are in turn followed by about five irregular crossbands that are often broken middorsally to give a series of lateral dark blotches. The ground color is gray dorsally and white ventrally. The two juveniles do not differ markedly from the adults as far as coloration or pattern.

Lazell described the female holotype in life as follows: "a dull-colored animal with a pattern composed of three basic hues – each tending to be unique on an individual scale. There are very irregular dark gray-brown blotches across the dorsum; beginning at the back of the head there are three such markings to the shoulders. There are three more crudely 'Y' shaped markings on the body, the most anterior of which bifurcates to the right, the remaining ones bifurcating to the left. There are two small blotches on the right side of the rump and one on the left. The second transverse blotch, on the nape, is broken by a light middorsal line that continues down through the fourth marking and then fades out. The ground color of the dorsum is ash gray. There are scattered over the dorsal surface short transverse series of white or partly white scales – from two to four in a row – that appear to have no correlation whatever with the rest of the animal's pattern. The top of the head is ash gray except for a very irregular, dark, gray-brown blotch on the parietal area. Coming back from the eye are two stripes, one of which runs downward across the cheek; the other nearly connects with the first transverse marking on the back of the head . . . Along each side of the animal is a line of partially connected, small, dark, gray-brown blotches; just ventral to this row is another composed of widely spaced, single dark, gray-brown scales."

Distribution: Known only from the type-locality (Fig. 1).

Remarks. S. shrevei is so very distinctive in having a blotched pattern that we are not really sure that it is at all closely related to the balance of the species in this group. Although, as will be shown later, some *S. leucaster* approach blotching to some extent, they do not have such a markedly blotched pattern as does *S. shrevei*. Comparisons with other taxa will be made in their appropriate places in the present paper.

Lazell (1961) stated that the holotype was taken from a large circular rock pile, the rocks varying in size from golf ball to nearly football size. The pile was of some age since several *Acacia* were growing from within it. The area at Môle St. Nicholas is arid. The new material was native-collected and we have no data on the habitat.

Specimen examined. Haiti, Dept. du Nord Ouest, Môle St. Nicholas (MCZ 62548 – holotype; ASFS V49555-56, ASFS V49586-87, ASFS V49769, ASFS V49831).

Sphaerodactylus rhabdotus Schwartz

Sphaerodactylus rhabdotus Schwartz, 1970, J. Herpetology, 4(1-2):64. *Type-locality:* 5 km SE La Florida, 500 feet (153 m), Independencia Province, República Dominicana. *Holotype:* USNM 166960.

Definition. An Hispaniolan species of *Sphaerodactylus* characterized by the combination of: 1) dorsal scales keeled and only slightly imbricate, a few small keeled scales in the shoulder region but no middorsal row of granules or small scales; 2) moderate number (36-44) of scales at midbody; 3) modally 2 internasal scales; 4) dorsal pattern of two dark brown lines on a pale ground, these lines not interrupted by white dots or spots; a brownish occipital Y usually present (Fig. 2).

Distribution. República Dominicana, Independencia Province, from near Las Lajas on the Dominico-Haitian border, east to the vicinity of Angostura, and occurring on both the north and south sides of Lago Enriquillo (Fig. 1).

Variation. There are 27 specimens of *S. rhabdotus*; the largest male (USNM 166960 – holotype) has a snout-vent length of 31 mm, the largest female (ASFS V20486) 32 mm. Scale counts on the series are: dorsal scales between axilla and groin 20-28 ($\bar{x}$ = 23.8); ventral scales between axilla and groin 24-31 (28.0); midbody scales 36-44 (40.4); supralabials to mid-eye modally 4/4 (23 individuals) but other counts of 4/5 (2), 4/6 (1), and 5/5 (1); internasals modally 2 (17 individuals), but other counts of 1 (2) or 3 (8); fourth toe lamellae 9-12 (10.1; M_O = 9 – 36%); escutcheon 5-9 X 7-25. In life, the dorsal ground color varies from pink (almost lavender) to very pale gray; the dorsolateral lines are brown to black, these lines usually entire and without interruption (but see beyond). An occipital Y is present but variable in expression (i.e., from clear and distinct to somewhat blurred); the stem of the Y may lead to a median dorsal brown line so that the dorsum appears trilineate. Males have the head and snout yellow in life, and adults of both sexes have the tail yellow; this latter feature is more pronounced in males than in females. The iris has been recorded as brown with a golden pupillary ring, or gray. There may be a few irregularly placed middorsal small, nongranular scales, especially in the shoulder region at the zone of transition from the granular nuchal scales and the large dorsals.

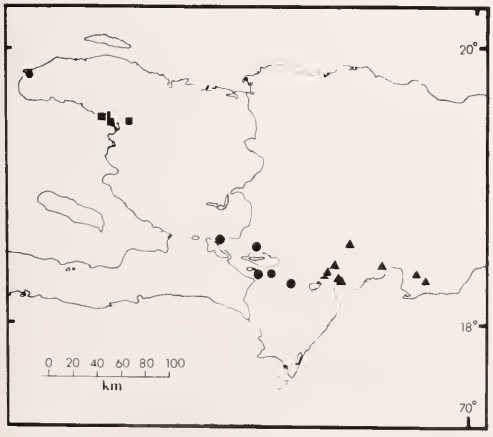

Fig. 1. Hispaniola, eastern Haiti and western República Dominicana, showing the known distributions of *Sphaerodactylus* of the *shrevei* group: hexagon, *S. shrevei*; squares, *S. asterulus*; circles, *S. rhabdotus*; triangles, *S. leucaster*. Some localities for *S. asterulus* have been omitted for clarity.

Comparisons. As far as size and scutellation are concerned, the differences between *S. shrevei* and *S. rhabdotus* are slight. Females reach about the same snout-vent lengths (30 mm in *S. shrevei*, 32 mm in *S. rhabdotus*). Means of dorsals in axilla-groin distance are the same (23.8). However, *S. shrevei* averages higher in number of ventrals (32.2 versus 28.0) and midbody scales (42.0 versus 40.4). In the latter count, the scale counts of the two species overlap broadly, whereas in the former the counts overlap but slightly (31 – 33 in *S. shrevei*, 24 – 31 in *S. rhabdotus*). The single internasal in *S. shrevei* differs from the 2 internasals in *S. rhabdotus*; the modes in each case are strong. But the two species differ amply in dorsal pattern and coloration; *S. shrevei* is a blotched lizard and lacks an occipital Y, whereas *S. rhabdotus* is lineate and has an occipital Y. The hues involved in both cases are distinctive. *S. rhabdotus* is a pallid lizard, dorsally striped with brown on a pale pink to lavender ground, in contrast to the gray dorsal color and blotched pattern of *S. shrevei*.

The dorsal pattern of *S. rhabdotus* is quite constant. But there is one specimen

(TCWC) that requires comment. This individual (male, snout-venth length 26 mm) has the dorsolateral brown lines so broken as to cause them to form a series of dots. Although not all specimens of *S. rhabdotus* have the lines absolutely complete, this individual is at the extreme condition. Faded specimens of *S. leucaster*, which has the dorsolateral lines interrupted by (in life) white, starlike blotches, assume this same pattern (i.e., the white pigmentation fades leaving only broken dark lines). This specimen (TCWC 50162) thus superficially resembles preserved specimens of *S. leucaster*; whether in life it had white spots in the breaks in the dorsolateral stripes is unknown. If so, it would certainly re-enforce the relationship of *S. rhabdotus* and geographically close *S. leucaster* and would suggest that these two species are in actuality subspecies. At present their ranges are known to be complementary, but they differ in dorsal pattern. Perhaps these differences are at the subspecific level, but we are unwilling as yet to take that taxonomic step.

The type series was collected in the fallen thatch of a construction-crew shack at the northern base of the Sierra de Baoruco. The lizards were relatively abundant in the thatch, especially at the interface between the thatch and the limestone base upon which it was resting, and within the dry, folded, accordion-like bases of the palm fronds. The specimen from near Angostura was taken from beneath a piece of dry palm siding at an old and abandoned shack near a gypsum mine. The Duvergé lizard was found in an old pile of palm trunk cuttings in xeric scrub. The senior author has never collected *S. rhabdotus* in a "natural" situation, despite search for it in the xeric Valle de Neiba.

Specimens examined. República Dominicana, Independencia Province, 1 km ESE Las Lajas, 75 m (UF/FSM 42920); 5 km SE La Florida, 153 m (USNM 166960 – holotype, USNM 166961-62, CM 45890-92, MCZ 92096-98, ASFS V17180, ASFS V20485-87, ASFS V20797-98); 6 km NW Duvergé (RT 4421); 2.0 km E La Descubierta, 15 m (TCWC 50161-69); 11 km SE Angostura (ASFS V41298).

Sphaerodactylus leucaster Schwartz

Sphaerodactylus leucaster Schwartz, 1973, Proc. Biol. Soc. Washington, 86 (4):36. *Type-locality:* El Iguito, 1.6 mi. (2.6 km) NE Fondo Negro, Barahona Province, República Dominicana. *Holotype:* USNM 189234.

Definition. An Hispaniolan species of *Sphaerodactylus* characterized by the combination of: 1) dorsal scales keeled and slightly imbricate, with a few smaller scaled middorsally; 2) moderate number (35-46) of scales at midbody; 3) modally 2 internasal scales; 4) dorsal pattern of 2 dark brown dorsolateral and 2 broken ventrolateral stripes on a lavender ground, the dorsolateral stripes with from 4 to 7, relatively large, discrete white spots per stripe; 5) males with a median dark brown nuchal line, females with a dark brown cephalic-nuchal Y (Fig. 2); heads and throats bright orange and tails yellow in males.

Distribution. República Dominicana, the extreme eastern portion of the Valle de Neiba, extending thence eastward as far as the vicinity of Baní, Peravia Province, in the Llanos de Azua (Fig. 1).

Variation. There are 19 specimesn of *S. leucaster*; the largest male (ASFS V40797) has a snout-vent length of 27 mm, the largest female (ASFS V35639) 31 mm. Scale counts on the series are: dorsals between axilla and groin 19-29 ($\bar{x}$ = 23.5); ventral scales between axilla and groin 20-32 (27.4); midbody scales 35-46 (39.8); supralabials to mid-eye 4/4 (15

individuals), 3/3 (2), and 5/5 (2); internasals modally 2 (13 individuals) or 1 (6); fourth toe lamellae 7-11 (9.5; M_O = 10 – 44%); escutcheon 5-8 X 8-24. The dorsal color in life is lavender, with, in males, the head bright orange; there is a pair of dorsolateral dark brown lines that begin behind the eyes and extend onto the base of the tail. Ventral to these, there is a pair of lateral dark brown lines. The dorsolateral lines in life are broken by a series of distinct white blotches; in preserved specimens these white blotches disappear (due in part at least to the general pale dorsal color) with the result that the dorsolateral lines appear merely broken. The venter is flesh-colored, and the tail yellow in males. Some specimens have a vague median nuchal line which may lead to a pair of arms extending onto the head, to form an occipital Y. Females are patterned like males except that the head is not orange, and there may be some dark brown stippling on the throat. There are a few scattered smaller scales middorsally.

Comparisons. S. leucaster most closely resembles *S. rhabdotus* in both coloration and lineate pattern. The major pattern difference between these two species is the presence of the white spots in the dorsolateral lines of *S. leucaster* to give a broken effect. From *S. shrevei*, *S. leucaster* differs in being lineate and not blotched (but see below). Scale counts between *S. leucaster* and *S. rhabdotus* are comparable. *S. shrevei* lies at the upper extreme of *S. leucaster* in midbody scale counts, and the mode in *S. shrevei* is one internasal (71%) a condition observed in about one-third of the *S. leucaster* examined. The iris in *S. leucaster* is greenish gold, and brown to gray in *S. rhabdotus*; there are no data on the iris color in *S. shrevei*.

Remarks. We have already commented on the possibility that *S. rhabdotus* and *S. leucaster* should be regarded as subspecies. The two closest localities for the species are 11 km SE Angostura, Independencia Province, and 2 km NE Canoa, Barahona Province – a distance of 21 km. The presence of a single specimen of *S. rhabdotus* from near La Descubierta having a pattern similar to that of *S. leucaster* suggests that there is genetic continuity between the two taxa. But this is slim evidence at best, and neither species is represented from many localities or in series.

Perhaps the most interesting phenomenon in *S. leucaster* occurs in three specimens from the eastern and northern extremes of the range. Four specimens require comment.

ASFS V35790 was brought to the senior author with a long series of *S. ocoae* Schwartz and Thomas, from north of Cruce de Ocoa. It was not noted as being different in coloration or pattern from that species at the time of its acquisition, and thus no color notes were made on it in life. Only under the microscope was it obvious that this individual was a *shrevei* group member (and at that time the easternmost specimen). It differs from other *S. leucaster* in lacking dorsolateral lines and white spots; rather, the dorsum is dotted with dark brown on a brown ground. It is an adult female with a snout-vent length of 29 mm.

A second noteworty specimen is UF/FSM 36964, a female with a snout-vent length of 26 mm. This specimen is from near Cortés in Azua Province, and thus from the northeastern extreme of the range. It is like the specimen described above, although there are distinct remnants (much broken) of four dorsal lines with some white flecking still distinct on the head (but not the body).

UF/FSM 42926 is a female with a snout-vent length of 28 mm. This specimen is from 2 km NE Baní, the extreme eastern limit of *S. leucaster*. The dorsal

pattern is without any obvious lineate configuration but is rather blotched with large dark blotches, very similar to the condition in *S. shrevei*. Color notes by Fred G. Thompson state that in life the ground color was light grayish blue, head and tail orange, venter more gray than blue, and diffuse black spots on the dorsum. All three of these specimens mentioned lack a nuchal Y.

A fourth specimen is less peculiar; it is ASFS V35638, a male with a snout-vent length of 26 mm, from the type-locality. In this individual, the dorsolateral lines are very broad and broken into a series of dark blotches. The occipital Y is present. The lizard is distinctive only in the width of the dorsolateral lines and the approach to a blotched condition, although the blotching is much less obvious than in UF/FSM 42926.

The significance of these peculiar variants is prolematical. In each case except the last, there is only one specimen from a locality. Whether there are other species (or subspecies of *S. leucaster*) in the eastern portion of the area we attribute to *S. leucaster* remains undetermined. Yet from, or between, some of these localities, there are specimens that are typical *S. leucaster*. None of the prolematical specimens is maximally sized. The senior author has tried repeatedly to secure additional specimens at the locality for ASFS V35790 (3 km N Cruce de Ocoa, Peravia Province), without success. In fact, the area is oasis-like in an otherwise very xeric region, not the typical situation for a member of the *shrevei* group. More likely, the local *S. leucaster* population occurs in the adjacent desert areas, where it may be difficult to secure additional specimens.

Aside from the highly specialized situation at the type-locality, *S. leucaster* has been taken in an abandoned termitarium and under the bark of a large, standing, old *Acacia* near the base, both in xeric coastal woods, and under limestone boulders on a xeric hillside. Fred G. Thompson secured specimens in the dead basal rosettes of *Agave*.

Specimens examined. República Dominicana, Barahona Province, 2 km NE Canoa, 50 m (UF/FSM 42924); 3 km NE Canoa, 110 m (UF/FSM 42921); 13 km ESE Canoa (UF/FSM 42922-23); 15 km ESE Canoa (ASFS V40797-98); El Iguito, 2.6 km NE Fondo Negro (USNM 189234 – holotype, ASFS V30524-26, ASFS V35637-40); *Azua Province*, 2 km NW Cortés, 240 m (UF/FSM 36964); 3.5 km SSE Azua, 30 m (UF/FSM 42925); 5.3 km ESE Azua (USNM 197338); *Peravia Province*, 3 km N Cruce de Ocoa, 153 m (ASFS V35790); 2 km NE Baní, 100 m (UF/FSM 42926).

Sphaerodactylus asterulus, new species

Holotype. CM 60521, an adult female, from 9.3 km W Ça Soleil, 92 m, Département de l'Artibonite, Haiti, one of a series collected 20 June 1978 by Eugene D. Graham, Jr., and Albert Schwartz. Original number ASFS V45996.

Paratypes (all from *Dépt. de l'Artibonite, Haiti*). ASFS V45971-95, ASFS V45997-6012, same data as holotype; ASFS V45935, Terre Sonnain, 1.6 km N Les Poteaux, 122 m, 7 August 1977, native collector; ASFS V46015, 7.7 km W Ça Soleil, 30 m, 20 June 1978, E.D. Graham, Jr.; ASFS V46338-49, Lapierre, 7.6 km W Ça Soleil, 122 m, 9 July 1978, native collectors; ASFS V46503-12, Lapierre, 7.6 km W Ça Soleil, 122 m, 10 July 1978, native collectors; ASFS V46588-91, 5.6 km W Ça Soleil, 11 July 1978, native collectors; ASFS V46603-13, 15.9 km W Ça Soleil, 11 July 1978, native collector; ASFS V46615-19, 9.3 km W Ça Soleil, 11 July 1978, native collectors; ASFS V46691-93, 12.2 km W Ça Soleil, 12 July 1978, native collectors; ASFS V46768-93,

12.2 km W Ça Soleil, 14 July 1978, native collectors; ASFS V46594, ASFS V48012-119, Lapierre, 7.6 km W Ça Soleil, 122 m, 11 July 1978, ASFS V46697. ASFS V48200-10, ASFS V48221-97, RT 5618-63, AMNH 115517-31, ANSP 27170-79, CM 60522-36, KU 93393-402, MCZ 132392-400, UF/FSM 21587-600, USNM 197339-55, Lapierre, 7.6 km W Ça Soleil, 122 m, 12 July 1978, native collectors.

Definition. An Hispaniolan species of *Sphaerodactylus* characterized by the combination of: 1) dorsal scales keeled and slightly imbricate, without a middorsal row of small scales; 2) low number (33-42) of scales at midbody; 3) modally 2 internasal scales; 4) dorsal pattern of two dark brown dorsolateral and two dark brown lateral lines on a purplish tan ground color, the dorsolateral lines with a series of tiny white dots, each encompassing a granule (on the neck) or a portion of a dorsal scale (on the body), these white dots numbering as many as 12 on each side; 5) a dark brown nuchal Y, which may disappear or become more diffuse with increasing size or darker ground color, the Y most often represented only by its stem in males, complete in females (Fig. 2); 6) heads yellowish to yellow in males, only faintly yellowish in females, throat and tails bright yellow in males; 7) often with some sort of stippled, lineate or reticulate dark throat pattern in both sexes; more pronounced and frequent in males.

Description of holotype. An adult female with a snout-vent length of 30 mm and a tail length (distal three-quarters regenerated) of 22 m. Scale counts are: dorsals between axilla and groin 31, ventrals between axilla and groin 31, scales around midbody 40, fourth toe lamellae 12, supralabials to mid-eye 4/4, 2 internasals. Dorsal scales subimbricate to not imbricate, keeled; ventral scales smooth, imbricate, cycloid. Dorsum in life pale tan to purplish tan with a pair of dark brown dorsolateral stripes from level of the upper margin of the eye onto the unregenerated base of the tail, a pair of similarly colored lateral stripes from about the level of the upper lip posteriorly above the forelimb insertion to above the hindlimb insertion, much less clear on the base of the tail, and the vague

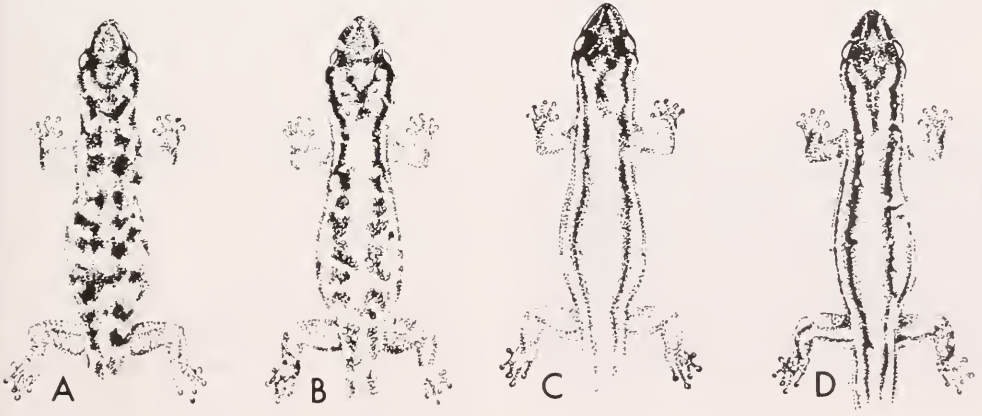

Fig. 1. Hispaniola, eastern Haiti and western Republica Dominicana, showing the known distributions of *Sphaerodactylus* of the *shrevei* group: hexagon, *S. shrevei*; squares, *S. asterulus*; circles, *S. rhabdotus*; triangles, *S. leucaster*. Some localities for *S. asterulus* have been omitted for clarity.

remnants of a third pair of lines low on the sides separating the dorsal tan ground color from the grayish flesh-colored venter; a nuchal Y present but very diffuse, the stem abbreviated; a series of white dots in the dorsolateral lines beginning on the postocular granules (where each spot is restricted to a granule) and proceeding posteriorly, about 6 dots on each side; fore- and hindlimbs mottled with shades of brown to tan; head faintly yellowish and without distinct pattern except for dark lores and dark upper surface.

Variation. Of the series of 448 *S. asterulus*, the complete suite of counts has been taken on 63 specimens; counts of supralabials and internasals, and snout-vent length measurements only were taken on the remaining specimens. The largest male (RT 5628) has a snout-vent length of 31 mm, the largest females (ASFS V46776, ASFS V48123) 31 mm. Scale counts are: dorsals axilla to groin 17-24 ($\bar{x}$ = 21.4); ventrals axilla to groin 25-33 (28.6); midbody scales 33-42 (37.2); supralabials to mid-eye 4/4 (414 individuals), 3/3 (2), 3/4 (2), 4/5 (25), 5/5 (3); internasals 2 (266 individuals), 1 (50), 3 (107), 4 (2); fourth toe lamellae 8-12 (10.2; M_O = 10 – 37%); escutcheon 1-9 X 6-21.

Fig. 3. The type-locality of *S. asterulus* (9.3 km W Ça Soleil, Dept. de l'Arbonite, Haiti); from a Kodachrome slide taken by Eugene D. Graham, Jr., 14 July 1978.

In such a long series, including large numbers of males, females, subadults, and juveniles, it is not surprising that there is great variation in dorsal color and pattern. As a general statement, males are pale purplish tan dorsally, with 2 dark brown dorsolateral lines and a pair of lateral brown lines, to give a generally tetralineate effect; in addition to these lines, there is a ventrolateral pair, that are diffuse or broken, at the junction of the dorsal and ventral colors; the dorsolateral lines have as many as 12 tiny white dots enclosed within them, these dots encompassing a single granule on the neck region (where there may be 3 or 4 white dots crowded together) and only a portion of a dorsal scale on the body. These white dots are tiny but nevertheless quite conspicuous in life against the brown stripe. The cephalic Y is present but in males may be reduced to only its stem as a short middorsal nuchal dark brown line. The heads of males are yellow to yellowish, and the throats are bright yellow as are the tails. The venter is grayish flesh-colored, in sharp contrast to the yellow throat.

Females are basically like the males in dorsal pattern but usually with a complete cephalic Y; the heads are at times only faintly yellowish. The general female dorsal aspect is paler than that of males, more contrastingly lined, and the dorsal ground color tends towards tans without purplish tints. The iris in both sexes is yellow.

Juveniles are patterned like females, but the ground color is paler, and the lines are all more distinct. In juvenile specimens the ventrolateral pair of lines may be as distinct and entire as the dorsolateral and lateral lines, or they may be fragmented and incomplete as described for the holotype.

The dorsolateral lines are common to most of the series. In some females, the

contrast between the lines and the ground color is not so intense as in other females, and the occipital Y is either incomplete (represented by its stem only) or diffuse and almost concolor with the dorsal cephalic brownish color. Throats in both sexes may be immaculate. This is the common condition in males, whereas in many (but not all) females there may be vague indications of a grayish reticulum or grayish stippling on the throat. In subadult females the dark loreal line and a dark median snout line are present, but these are obscured with increased size. There is little tendency for the dorsolateral lines to break up into a series of blotches (as in *S. shrevei*), and the lines are almost always entire. Occasional specimens show a tendency toward fragmentation but these are rare. If so, the dorsolateral line fragments are not blotchlike and are recognizable as parts of dorsolateral lines, not independent blotches.

The most distinctive feature of *S. asterulus* is also the most variable in preserved specimens: the tiny white isolated dots in the dorsolateral lines. In our original series of 42 specimens, our color notes state that *all* specimens (23 males with snout-vent lengths between 22 and 29 mm; 18 females with snout-vent lengths between 21 and 30 mm; one hatchling with a snout-vent length of 15 mm) had dots present in the dorsolateral lines. When these (and the remainder of the long series) were studied approximately 4 months later, most of both sexes still showed the white dots or the scales where they had been, but they were less often encountered in males (53%) than in females (86%). Most persistent are the dots on the granular neck scales, with those on the body tending to become obscure or lost. Since preserved *S. leucaster* completely lose their white "stars" promptly after preservative, we can logically assume that the same is true for *S. asterulus* and its dots. A second factor is that the dots in *S. asterulus* tend to be less clear and bold in large specimens. Both these factors, then, would tend to account for the loss of white dots in such a large percentage of *S. asterulus*. (It is interesting that juveniles with snout-vent lengths of 19 mm or less retain spots clearly.) But these factors do not account for the fact that almost half of the male *S. asterulus* (47%) have lost their dots, whereas a much smaller percentage (14%) of the females has done so. We suggest that there is some weak dichromatism in *S. asterulus* with more males than females tending toward an unspotted condition in life, and that by chance our original series had all males with dots.

Comparisons. Sphaerodactylus asterulus is geographically close to *S. shrevei* (80 km) across the Presqu'île du Nord Ouest and is patterned similarly to *S. leucaster*, from whose range *S. asterulus* is removed from 220 km. From *S. shrevei*, *S. asterulus* differs in having a lined dorsum in contrast to a blotched or crossbanded one. *Sphaerodactylus shrevei* averages higher in all scale counts (dorsals 23.8 versus 21.4 in *S. asterulus*; ventrals 32.2 versus 28.6 in *S. asterulus*; midbody scales 42.0 versus 37.2 in *S. asterulus*), although all counts overlap broadly with least overlap in number of dorsals. The modally 1 internasal in *S. shrevei* differs from the modally 2 internasals in *S. asterulus* (71% versus 60%); 50 of 445 (11%) *S. asterulus* have 1 internasal.

S. asterulus and *S. leucaster* are in some ways similar – both have dorsolateral lines with white inclusions – dots in the former case, large radiating white spots in the latter. In *S. leucaster*, the white spots interrupt the dorsolateral lines completely, resulting in irregularly broken dorsolateral lines, whereas this is not the case in *S. asterulus*. *S. asterulus* also has well

developed lateral stripes, which are absent in *S. leucaster*. Scale counts and frequencies are comparable.

From *S. rhabdotus*, *S. asterulus* differs in having dots in the dorsolateral lines, whereas *S. rhabdotus* has neither spots or dots – the lines are entire (see, however, the discussion of *S. rhabdotus* variation in the present paper).

S. asterulus has a lower mean in dorsal scales (21.4) and midbody scales (37.2) than either *S. leucaster* (23.5 and 39.8) or *S. rhabdotus* (23.8 and 40.4). On the other hand, *S. asterulus* has a higher ventral mean (28.6) than either *S. leucaster* (27.4) or *S. rhabdotus* (28.0). In all cases the ranges of variation overlap broadly. Two internasals show about the same frequency in all three species (*S. asterulus* 60%, *S. leucaster* 68%, *S. rhabdotus* 63%). Both *S. asterulus* and *S. leucaster* have modes of 10 subdigital lamellae, whereas *S. rhabdotus* has a mode of 9. The modes are weak (37% and 44% in the first two species, 36% in *S. rhabdotus*). Means of fourth toe lamellae vary from 9.5 in *S. leucaster* to 10.2 in *S. asterulus*.

Escutcheon size in males of all three species is peculiar in its extreme variability. In *S. asterulus*, the length varies from 1 to 9 scales, and the width from 6 to 21 scales. The length of the escutcheon in male *S. leucaster* (5-8) and *S. rhabdotus* (5-9) is much less peculiar, but in these two species the width of the escutcheon shows extreme variability, from 8-24 in *S. leucaster* and 7-25 in *S. rhabdotus*. Ontogeny and sexual maturity may be factors in this case.

Members of the *shrevei* complex have only hair-bearing scale organs. In *S. asterulus* the number is extremely variable, with between 6 and 15 organs along the free margin of the scale, each with from 1 (usually) to 2 or 3 "hairs." *S. rhabdotus* has 5 to 11 hair-bearing organs, each with 1 "hair," per scale (Schwartz, 1970:64) and *S. leucaster* has 3 to 8 organs, usually with 2 "hairs" (Schwartz 1973:36).

Remarks. We have already mentioned the taking of the original series of *S. asterulus* within the dead basal rosettes of *Agave* and in low rock piles. In the debris in the *Agave* leaves we also encountered many eggs, mostly hatched, but five unhatched. Measurements of four of these vary (in mm) between 6.4-6.8 X 5.1-5.7. The fifth egg hatched in the collecting bag, and the juvenile from it has a snout-vent length of 15 mm. In addition to the large numbers of *S. asterulus* encountered by us, we also secured an adult *Epicrates f. fordi* Gunther and an immature *Phyllodactylus*. The snake was within the punky stem of an *Agave*, whereas the lizard was in a pile of rocks and *Agave* leaves.

DISCUSSION

The *shrevei* group is composed of four species whose range occupies two general regions: extreme northwestern Haiti and the Valle de Neiba and the Llanos de Azua in the Republica Dominicana. Those authors who have previously dealt with members of the group (Lazell, 1961; Schwartz, 1970, 1973) have been hard pressed to suggest to what other Hispaniolan or even Antillean geckos the *shrevei* group is related. The combination of characteristics of the *shrevei* group set it off from all other *Sphaerodactylus*; the convex snout and vertically elliptical pupils are, in combination, unique. These characters are apparently primitive within *Sphaerodactylus*, and it may well be that the *shrevei* group represents an old remnant of a *Sphaerodactylus* radiation. Its apparently fragmented distribution would tend to confirm this interpretation. It is also possible that the *shrevei* group is derived from the *difficilis* complex, which

is in turn composed of the Hispaniolan members of the *notatus* group. We make this latter suggestion, not for any particular reasons of similarity between the two (although at least keeled dorsal scales is one character in common between them), but only because the *difficilis* complex is the most widespread and most diverse of the Hispaniolan groups and/or complexes of geckos. Although the *difficilis* complex lizards do not totally shun xeric regions, they are not the "typical" geckos occupying xeric areas. Thus the *shrevei* group and the *difficilis* complex are roughly complementary in distributions. One member of the *difficilis* complex, *S. altavelensis* Noble and Hassler, is a xerophile, and it has been taken sympatrically with *S. asterulus*; another member, *S. cryphius* Thomas and Schwartz, was found in the same thatch pile as the type series of *S. rhabdotus*. *Sphaerodactylus ocoae* Schwartz and Thomas also appears to be at least marginally sympatric with *S. leucaster*, and *S. difficilis* Barbour and *S. leucaster* may well be sympatric in portions of the Llanos de Azua. A still-unnamed species of *Sphaerodactylus*, not of the *difficilis* complex, has been taken with *S. asterulus*. Despite the above examples of macrosympatry and even syntopy, but on the other hand taking into consideration the large number of Hispaniolan *Sphaerodactylus* species, we can say as a general statement that members of the *shrevei* group are so confirmedly xerophiles that they are rarely found with other Hispaniolan *Sphaerodactylus*.

It would be most convenient to state that the two northern species (*S. shrevei* and *S. asterulus*) were more closely related to each other than they are to the southern pair (*S. rhabdotus* and *S. leucaster*: see Fig. 1). This seems not to be the case; the lineate pattern of *S. asterulus*, *S. rhabdotus*, and *S. leucaster* would seem to ally them to each other, despite the wide hiatus between them, rather than the blotched pattern of *S. shrevei* and the dotted pattern of *S. asterulus*. Even more convincing of this relationship are the white dots of *S. asterulus* and the white blotches of *S. leucaster*. In fact, one might with some justification consider *S. asterulus* a subspecies of *S. leucaster* on this basis. But the wide geographical separation of these two taxa, plus the interposition between them of *S. rhabdotus* (which lacks white markings in the dorsolateral lines) suggests that we are dealing with three species. We have commented on the complementarity of the ranges of *S. leucaster* and *S. rhabdotus* and the possibility that perhaps these two taxa might better be regarded as subspecies; certainly the 21 km gap between their known ranges is small. But between them courses the large Río Yaque del Sur, a major river, and *S. leucaster* occupies areas east of the river and *S. rhabdotus* the west.

Williams (1961) noted that the Hispaniolan herpetofauna is divided into two major sections, corresponding to the north and south paleoislands into which modern Hispaniola was divided. This point has been emphasized repeatedly by other authors, and it is a valid one. Although there are exceptions, most of the Hispaniolan herpetofauna can be divided into north and south island elements; the modern division of these two old islands is the Cul de Sac-Valle de Neiba plain, and it is in the latter portion of this (the Valle de Neiba) that *S. rhabdotus* occurs. There is no question that the *shrevei* group as a whole is north island in affinities: three of its species (*S. asterulus*, *S. shrevei*, *S. leucaster*) occur exclusively upon it. But *S. rhabdotus*, originally described from a south island locality, has now been taken on both sides of the Valle de Neiba; two localities (Las Lajas; La Descubierta) are on the

northern side, whereas three others (La Florida; Duvergé; Angostura) are on the south. If we postulate that *S. rhabdotus* and *S. leucaster* were originally inhabitants of the southern xeric shore of the north island, the two species separated by the north island Río Yaque del Sur, then it is probable that, with closure of the interisland strait, *S. rhabdotus* has crossed the Valle de Neiba to reach to the foothills of the Sierra de Baoruco on the south island. Such a scenario presents no major problems and accounts for the occurrence of *S. rhabdotus* away from the north island center of the group.

S. shrevei and *S. asterulus* are apparently restricted to northwestern Haitian Presqu'île du Nord Ouest, the former on the peninsula itself, the latter at its southeastern base. Most of this peninsula remains unknown herpteologically, and we have as yet no clear concept of what species occur there or the precise distributions of the species already known. Most of the latter are known from very limited material and from a few scattered localities (or only one locality). What is puzzling are the radical differences in pattern between *S. shrevei* and *S. asterulus* – blotched in the former, lineate in the latter. Thus, *S. asterulus* much more closely resembles in pattern the more distant *S. rhabdotus-S. leucaster* pair than it does adjacent *S. shrevei*. This may only mean that *S. shrevei* has been isolated for a much longer period from the basal, lineate *shrevei* group stock than has *S. asterulus*. Until more material of both species is known from this region, it is futile to speculate further. We should also like to point out that the road between the main road near Les Poteaux and the northern coast at Port-de-Paix passes through xeric country for much of its 77 km; only toward its northern coastal section near Port-de-Paix may the area be called mesic. Yet we had no success in securing *shrevei*-group geckos along this road. We did encounter *S. difficilis* at several xeric localities, which suggests that no *shrevei*-group member occurs here. But since *shrevei* group sphaerodactyls occur in very rigorous situations and may not be common, our not securing any in this region may not be so significant.

The 130 km hiatus between *S. asterulus* and *S. rhabdotus* may be more apparent than real. *Sphaerodactylus rhabdotus* is still known from the Haitian Cul de Sac plain, although it occurs very near the border (Las Lajas). We confidently expect it in this valley. From the western end of the Cul de Sac, xeric coastal areas follow the shore of the Golfe de la Gonâve to near St. Marc. Just north of that city lies the wide (30 km) Vallée de l'Artibonite, presently irrigated and flooded for the cultivation of rice. Inland, however, the Vallée de l'Artibonite is xeric and could supply suitable habitat for a *shrevei* group member. North of the valley and southeast of the city of Gonaïves, there are once more extensive xeric areas which are continuous with the region where *S. asterulus* occurs. It would seem likely that *S. rhabdotus* occurs from the República Dominicana into the Cul de Sac plain and thence along the shore to the southern edge of the Vallée de l'Artibonite and that *S. asterulus* occurs as far south as the northern edge of this same valley. But efforts on our part and those of others to secure members of this group in this region have failed totally. In fact, the sphaerodactyl fauna of this region is poorly known. As in all desert regions, native cooperation is hard to encourage, and collecting on the part of the investigator is more than likely to reveal nothing for lack of suitable places to search. Certainly this entire region is one which deserves special attention as far as its *Sphaerodactylus* fauna is concerned.

ACKNOWLEDGMENTS

In addition to specimens in the Albert Schwartz Field Series (ASFS), we have examined material in the Carnegie Museum (CM), Museum of Comparative Zoology (MCZ), Texas Cooperative Wildlife Collection, Texas A and M University (TCWC), University of Florida, Florida State Museum (UF/FSM), and the National Museum of Natural History (USNM). We wish to thank the respective curators and their assistants for loans of material: Clarence J. McCoy, Ernest E. Williams, José P. Rosado, James R. Dixon, Walter A. Auffenberg, Peter Meylan, George R. Zug, and Ronald I. Crombie. In the field we have had the assistance of Danny C. Fowler, Mark D. Lavrich, John C. Lucio, James A. Rodgers, Jr., Bruce R. Sheplan, William W. Sommer, Michael H. Strahm, James B. Strong, and Richard Thomas. Father John Breslin made Lucio's and Sommer's stay at Môle St. Nicholas pleasant and was instrumental in their securing the fresh material of *S. shrevei*. Paratypes have been placed in some of the above collections and the American Museum of Natural History (AMNH), the Academy of Natural Science of Philadelphia (ANSP), and the Museum of Natural History, University of Kansas (KU). We have also examined specimens in the collection of Richard Thomas (RT). Some specimens of *S. rhabdotus* and *S. leucaster* were collected under the auspices of National Science Foundation grants G-7977 and B-023603 to the senior author. We are especially grateful to Fred G. Thompson and Ronald I. Crombie for keeping us abreast of their activities in the República Dominicana and for allowing the senior author to examine material promptly after it had been collected. The illustrations of the four *shrevei* group species are the work of Beryl Bayer to whom we are grateful.

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NATURAL HISTORY OF THE MAP TURTLES *GRAPTEMYS PSEUDOGEOGRAPHICA* AND *G. OUACHITENSIS* IN WISCONSIN

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ABSTRACT

Natural history data were collected from populations of *Graptemys ouachitensis* and *G. pseudogeographica* on the Mississippi River, Vernon County, Wisconsin, from 1972-1978. Clutches of eggs were incubated in the laboratory and field under various temperature regimens. Hatchlings were maintained in the laboratory for six years to study growth rates, size at reproductive maturity and sex ratio within clutches.

Examination of reproductive tracts of 50 females suggest that they lay two clutches of eggs annually. The average clutch size for *G. pseudogeographica* was 14.1 and for *G. ouachitensis*, 19.2. The courtship displays of male *G. ouachitensis* and *G. pseudogeographica* involve the drumming of the foreclaws against the ocular regions of the female. The two species differed in the number of contacts per "titillation" bout.

Nesting was observed from 18 May to 26 July. Nest temperatures were monitored continuously for one month in 1972. Incubation temperatures in the laboratory were shown to affect hatching success, number of scute anomalies, size of yellow head blotches, and sex determination in both species. A skewed sex ratio of five females per male was calculated from trapping results.

Stomach contents of adult females suggested that the food resources are being partitioned. Females do not begin feeding until after laying their first clutch of eggs for the season.

The primary function of basking is thermoregulatory, no aggressive interactions were observed between basking *Graptemys*. Grackles, *Quiscalus quiscala*, were observed removing leeches, *Placobdella parasitica*, from basking *Graptemys*. Nest predation by red fox, raccoon, and otter was observed.

INTRODUCTION

The false map turtle complex, *Graptemys p. pseudogeographica, G. o. ouachitensis, G. o. sabinensis* and *G. p. kohni* has perplexed taxonomists and confused ecologists since the time of the original descriptions (Vogt, in press). Ecological data involving *Graptemys* have often been based on populations that were inaccurately identified. I realized this problem while attempting to determine which species of this group occurred in Wisconsin. Specimens collected from the Mississippi River near Stoddard, Vernon County, indicated that all taxa listed above occur sympatrically in Wisconsin. In 1971 at the same locality I collected 26 clutches of eggs from unknown females. Laboratory incubation yielded hatchlings with morphological characteristics of each, suggesting that *pseudogeographica, kohni, ouachitensis* and *sabinensis* have been described from individuals of a single highly polymorphic species. Smith (1961: 150-151) suggested this as one hypothesis, having been confronted with the same problem with false map turtles in Illinois.

These species and subspecies have been defined primarily on differences in head markings (e.g. Cagle, 1953; Ernst and Barbour, 1972); using these criteria

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all "forms" were found to have emerged from the 26 clutches of eggs, in some cases more than one "species" or "subspecies" from a single clutch. Study of this taxonomic perplexity was begun in 1972 at the Stoddard site where the population of *Graptemys* is large, and accessible. Between June and August of that year a mark and recapture study was begun. Subsequent trips were made intermittently between April and November of 1972-1978. Although I was concerned primarily with systematics of the *G. pseudogeographica* complex, various aspects of the natural history of *Graptemys* were observed. The field study was complemented by a five year laboratory study wherein eggs were incubated and young raised. Courtship behavior, reproductive potential and growth rates were studied in both the field and laboratory. This paper deals primarily with the natural history of *G. ouachitensis* and *G. pseudogeographica*. Detailed analysis of the systematics, courtship behavior and resource partitioning are presented elsewhere (Vogt, 1978).

SYSTEMATIC RELATIONSHIPS AND DISTRIBUTION

Graptemys pseudogeographica was described by Gray (1831) from the Wabash River at New Harmony, Indiana. *Graptemys pseudogeographica* is found primarily in large stream systems of the Mississippi drainage and occurs from the St. Croix and Wisconsin rivers in northern and central Wisconsin and the upper Mississippi River in Minnesota southward through Louisiana and eastern Texas (Vogt, Bull. Carnegie Museum, in press).

Cagle (1953) described two new subspecies of *Graptemys pseudogeographica* from the southern United States: *ouachitensis* from the Ouachita River of Louisiana and *sabinensis* from the Sabine River on the Louisiana-Texas border. My studies (Vogt, 1978) show that these two subspecies constitute a separate species, *G. ouachitensis*, which occurs from the Mississippi and St. Croix rivers in Wisconsin and Minnesota, south through the Mississippi River basin into Louisiana, west to Lake Texoma, Oklahoma and east into Indiana and West Virginia.

THE STUDY AREA

My study area, referred to as Mississippi River Pool 8, extends 37.5 river km north of a dam at Genoa, Vernon County, Wisconsin, to a point north of La-Crosse (43°40' N latitude, 93°13' W longitude). The Root and Lawrence rivers are the main tributaries of this impoundment. Before construction of the lock and dam in 1930, the main river channel comprised the bulk of the water surface area: 12,597 ha of channel, 2,764 ha of slough, 4,606 ha of marsh and 1,383 ha of pond. Since the dam was closed in 1937, water in the channel rose 3.5 m creating 27,481 ha of open pool and 2,873 ha of feeder channels; the marshland was increased to 9,435 ha (Claflin, 1973). Much of the pool area was taken from what previously had been river bottom forest (Curtis, 1959), stumps of which still remain provide excellent basking site for the turtles and attachment sites for invertebrates. Timber-meadow in the study area was 56,810 ha in 1930, but in 1970 only 25,396 ha remained (Claflin, 1973).

Within this general area, study was concentrated on 230 ha within the perimeter defined by the intersection of Crosby Slough and the main channel to the north, Crosby Slough and Cook Slough to the south and the main channel to the west. Most nesting observations were made on two islands which border the main channel (Fig. 1).

The islands are characterized by expanses of open sand surrounded by trees

[*Populus deltoides* Marsh., *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern., *Acer negundo* L., *A. saccarinum* L., *Betula nigra* L. and *Ulmus americana* L.] and shrubs [*Salix* sp., *Amorpha fruticosa* L., *Parthenocissus inserta* (Kerner) K. Fritsch, *Vitis riparia* Michx. and *Cornus obliqua* Raf.]. The trees and shrubs are essential in maintaining the integrity of the island by limiting wind and water erosion.

Open sand is sparsely covered with a variety of herbs, the most common in the open sand being *Sporobolus cryptandrus* (Torr.) Gray, *Carex* sp., *Bromus tectorum* L., *Tradescantia ohiensis* Raf., *Verbascum thapsus* L., *Oenothera biennis* L., and *Lepidium densiflorum* Schrad. *Graptemys* frequently dig nests adjacent to these plants. Along the border of the sand and edge of the woods *Asclepias syriaca* L., *Barbarea vulgaris* R. Br., *Saponaria officinalis* L., *Mollugo verticillata* L. and *Cycloloma atriplicifolium* (Spreng.) Coult. were common. Some plants occur primarily in the woods but were found at the open sand-woods interface: *Rhus radicans* L., *Laportea canadensis* (L.) Wedd., *Urtica dioica* L., *Solanum dulcamera* L., *Lynchnis alba* Mill., *Polygonum convolvulus* L., *Erigeron annuus* (L.) Pers., *Equisetum arvense* L. and *Galium obtusum* Bigel. *Phalaris arundinacea* L. occurs along the edge of the water.

The shrubs and trees along the periphery of the islands as well as the herbaceous plants on the open sand help prevent the wind from eroding the sand and exposing nests, and provide cover for hatchling turtles as they move to the water.

The turtles feed on and in the common marsh aquatic plants found in shallow water. Near the nesting islands these are *Scirpus validus* Vahl, *S. fluviatilis* (Torr.), *Sagittaria latifolia* Willd., *Zizania aquatica* L., *Phalaris arundinacea* L., *Phragmites communis* Trin., *Sparganium americanum* Nutt. and *Carex* sp. In deeper water near the islands and in the feeding areas near the stumps *Potamogeton nodosus* Poir., *P. crispus* L., *P. americanus* C. & S., *P. foliosus* Far., *Heteranthera dubia* (Jacqu.) MacM., *Vallisneria americana* Michx., *Elodea* sp., *Nymphaea tuberosa* Paine, *Nelumbo lutea* (Willd.), *Spirodela polyrhiza* (L.), *Lem-*

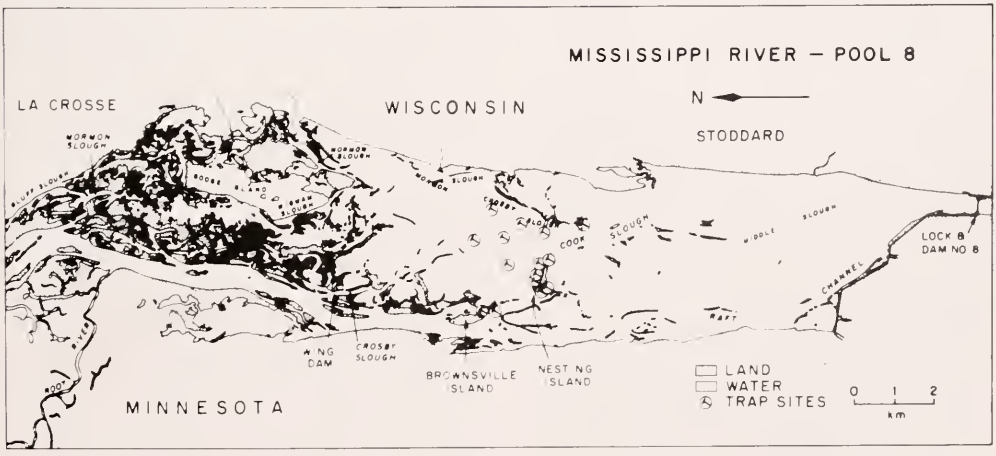

Figure 1. Topographic map of study area showing location of trap sites.

na minor L., *Wolffia columbiana* Karst., *Ceratophyllum* sp. and *Myriophyllum* sp. provide both food and shelter.

MATERIALS AND METHODS

Turtles were collected in fyke nets with leads, gill nets, and trammel nets and by hand capture (Vogt, Copeia, in press). Fyke nets varying in diameter from 61 cm to 90 cm and in mesh size from 2.54 cm to 5.08 cm were set in 1-1.5 m of water with the leads parallel to the shorelines of nesting beaches, between feeding grounds and deep water, or between basking logs and deep water. *Graptemys* was not attracted to bait, therefore fyke nets were baited with fresh dead carp only when turtles other than *Graptemys* were desired.

Local commercial fishermen, when setting gill nets in the study area, saved *Graptemys* that became entangled in the 12.5-17.5 cm mesh gill nets. Many of these were freshly drowned specimens from which eggs could be removed and incubated. These dead specimens were also used for stomach content analysis and skeletal preparation.

Trammel nets (5.08 cm mesh, 17.8 cm outer walling) were used primarily near basking logs or wing dams during hibernation periods (October, November, April). Turtles were driven into the nets by the use of a "carphorn" (Vogt, 1978).

Female turtles were hand captured on nesting beaches and by snorkeling while they were feeding. Hatchlings were collected in shallow water by hand and dipnet. Seining with a 60 m, 2.54 cm mesh bag seine proved to be ineffectual for obtaining young or adults.

During the first summer of study (1972) clutches of eggs from known females of *G. ouachitensis* and *G. pseudogeographica* were collected for taxonomic study. All six nesting beaches on the island were monitored each morning from 0500-0830 hrs (Central Standard Time) to obtain females and their recently laid egg clutches. Eggs from known females were measured by use of dial calipers accurate to 0.1 mm and incubated in the laboratory at 28°C. Each clutch was labeled and kept in a separate glass bowl containing moist spaghnum moss; and the entire bowl was enclosed in a clear plastic bag to prevent desiccation.

Following morning surveillance of nesting beaches, the 12 to 18 fyke nets, set at various localities within the study area, were checked (Fig. 1). All *G. pseudogeographica* and *G. ouachitensis* were brought back to camp for marking, and recording of data.

Each turtle was weighed, measured, photographed and marked; notes were made on shell injuries, abnormalities, color patterns and location of capture. Females were palpated for the presence of shelled eggs. Weight was determined to the nearest gram. The turtles were weighed under field conditions; upon handling *Graptemys* usually void their bladder. Injection of pilocarpin (Dorando, 1979) to induce voiding of all bladder water was not feasible or desirable since the inherent error was shown to be only 2.43% and any lasting effects on physiology or behavior of the turtle have not been studied. Maximum straight line carapace length, width and height were measured to the mm by use of a turtle measuring board (Cagle, 1946). Plastral measurements were taken either with dial calipers accurate to 0.1 mm or with a flexible ruler (nearest mm). Plastron width was taken at the suture between the axillary and pectoral scutes where it meets the 5th and 6th marginals. Straight line plastron length was taken from the farthest extension of the gular and anal scutes. During the summer of 1972 only carapace length and width were recorded. Both sides, dorsum, and venter of the head of each

turtle were photographed. Each turtle was individually marked with colored plastic plugs inserted with a "Dennison Buttoneer" through a 2 mm hole drilled through the center of one of the 7th-12th marginals on each side of the carapace. The marked turtles were then released at the site of capture the following day. Females were sacrified from April-November to obtain eggs and fresh reproductive tracts for determining reproductive condition. Notes were made concerning the number of growth rings on an abdominal scute when discernible. A ring was measured from the edge of the areola to the first deep groove in the scute. In agreement with Moll and Legler (1971) the term annulus is not used since it implies yearly rings and no proof exists to show if rings actually represent only one year.

Eggs were obtained by induction of oviposition by oxytocin injections (Ewert and Legler, 1978) during May and June of 1976 and 1977. If shelled eggs could be discerned by palpation, the females were taken back to the laboratory and injected intramuscularly with 10 units of oxytocin, then placed in a container of clean water, 25 cm deep at 28°-32°C and kept under bright lights with minimal disturbance. If eggs were not laid within one hr an additional injection of 10 units was given. Weights were taken before and after egg laying. The eggs were then weighed, measured and placed in moist vermiculite in incubators set at 25°, 30°, or 35°C or placed in a laboratory room where temperature was maintained at 32°C with a 14 hr light cycle. In 1977, individual eggs of seventeen clutches were incubated at these different temperatures.

Young from the 1972 year class have been reared in the laboratory to October 1978 (48 surviving) on a prepared diet of agar, gelatin, trout pellets, bone meal, oyster shells, cod liver oil, and multiple vitamins. This was done to compare growth rates between males and females and to determine if any changes in head color patterns occurred. They have been kept on a 14 hour light cycle at 32°. "Vitalities" (Durotest) were used to provide ultraviolet light. Blocks of plaster of Paris and copper tubing were kept in each tank to assist shell development. All the young hatched in 1972 were measured, weighed, marked and photographed in a manner similar to that used with adults. In addition, photographs were taken of the carapace and plastron. Measurements were repeated at least once a year. After the second year of growth, when external sex characteristics became apparent, males and females were placed in separate containers.

Analysis of feeding preference was made by examination of the stomach contents of freshly sacrificed or drowned individuals. Stomach flushing (Legler, 1977) was used during the 1977 season. Stomach contents from females were sorted and the components identified. Volume of the sorted contents was then determined by water displacement (Vogt, 1978). Feeding behavior of females was observed through a 30X spotting scope, or by snorkeling in their feeding areas.

Nest and body temperatures were taken with a Schultheis quick reading thermometer. An Easterline-Angus six-channel recorder with six thermistors was used for continuous recording of the temperature in four nests and the sand and air surface from July 16, 1972 through August 17, 1972.

All turtles sacrificed or drowned in the nets of commercial fishermen were either fixed in 10% formalin or skeletonized by dermestid beetles and deposited in the University of Wisconsin Zoological Museum, Madison. Hatchlings from 1971, 1972, 1976 and 1977 were also preserved and deposited there.

Table 1 = Measurements (cm) of carapace length (CL), carapace width (CW), carapace height (CH), and weight (g) of male and female *Graptemys* from Stoddard. (Range above; mean below)

Species	Sex	n	CL	CW	CH	WT (g)
G. ouachitensis	♂	68	10.9-13.7 (12.3)	8.7-10.3 (9.3)	4.0-5.2 (4.5)	161-309 (211)
G. psueodgeographica	♂	68	11.1-15.1 (13.3)	8.7-11.0 (10.0)	4.0-5.3 (4.7)	143-364 (251)
G. geographica	♂	45	9.3-13.6 (11.5)	7.6-11.1 (8.9)	3.4-4.6 (3.9)	165-350 (205)
G. ouachitensis	♀	265	16.3-24.2 (20.5)	12.7-19.1 (15.8)	6.5-10.2 (8.5)	557-2300 (1136)
G. pseudogeographica	♀	109	19.3-27.4 (22.5)	15.1-20.4 (17.3)	7.3-11.2 (8.8)	857-2502 (1477)
G. geographica	♀	15	20.1-25.8 (22.6)	14.9-18.7 (16.9)	7.5-9.4 (8.7)	761-1700 (1138)

REPRODUCTION

Sexual dimorphism

Sexual dimorphism is pronounced in all species of *Graptemys*. Males are much smaller in carapace length, width and height (Table 1). The male tail is comparatively much longer than that of the female, the distance from plastron to cloaca being greater in the male to facilitate intromission of the penis during copulation. The 2nd and 3rd foreclaws of male *G. ouachitensis* and *G. pseudogeographica* are disproportionately elongated. This characteristic has probably evolved along with their characteristic courtship display wherein the male drums his foreclaws over the ocular and otic regions of the female. The foreclaws of *G. geographica* males are not elongated and their courtship display does not involve foreclaw drumming.

Such a marked sexual dimorphism (males averaging 20% the mass of females) has many advantages. Most importantly it allows for intraspecific partitioning of food resources. Males feed on small, energy-rich insect larvae and mollusks, while the adult females are omnivores that feed on invertebrates and vegetation. Small size may allow males to put their energy into searching for females, precopulatory display and sperm production, rather than into growth. Laboratory studies show that reproductive maturity is reached in males at a smaller size allowing for a lower minimum age of reproduction (see section on laboratory growth, below).

Females, on the other hand, have an advantage in being large. The larger the female the greater the number of eggs she produces in a single clutch (Figs. 2 and 3). Warm spring temperatures allow oviducal application of the shell of the first clutch of eggs starting the last 10 days of May; then 10 days to 3 weeks to apply shell material to the second clutch, and an additional 10 days to three weeks for a possible third clutch. This is the maximum number of clutches since temperature becomes too low for incubation to be completed by the onset of winter. A larg-

er female provides a higher than average reproductive input into the population. In addition the larger size of the females may afford greater protection from avian and mammalian predators when they venture ashore to nest.

Reproductive cycles

Females begin the reproductive cycle from late June to mid-July after laying their last clutch of eggs for the year. From then until early September females feed and bask, converting the energy obtained into enlarged ovarian follicles. They enter hibernation with the coelomic cavity encroached upon by enlarged ovarian follicles. They do not feed in the spring until the first clutch has been laid. Mating probably takes place either in October or April while the turtles are congregated at

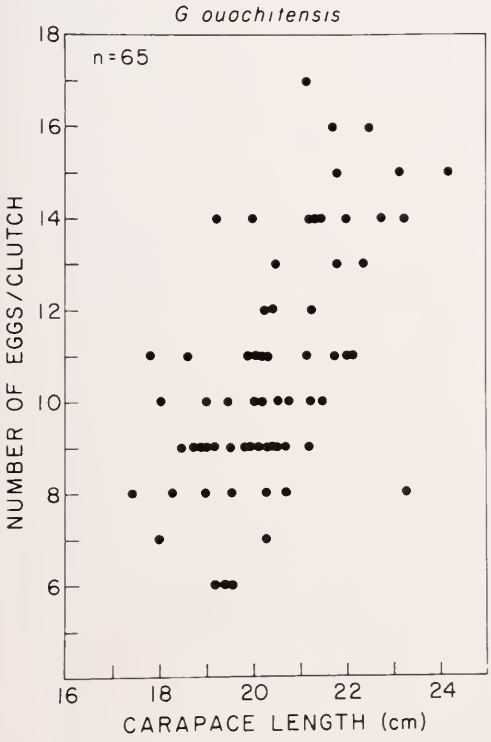

Figure 2. Relationship between carapace length of female and number of eggs per clutch in *G. ouachitensis.*

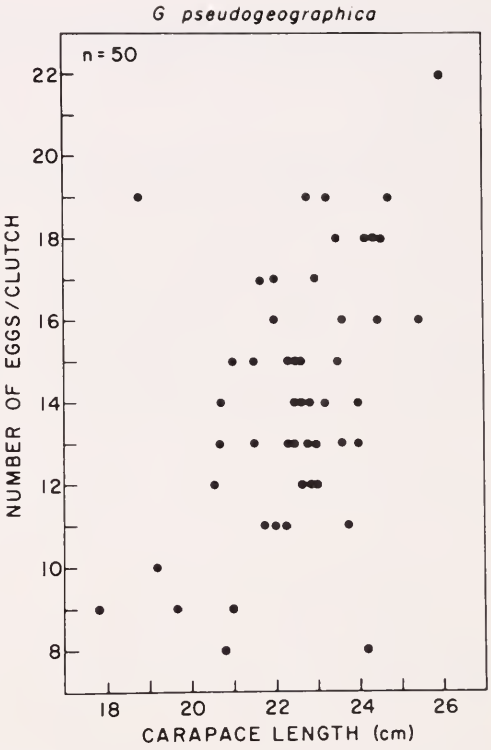

Figure 3. Relationship between carapace length of female and number of eggs per clutch in *G. pseudogeographica.*

hibernacula. After leaving the hibernacula in April the females move toward the nesting beaches and spend approximately six weeks basking and applying shell to ovarian follicles, and egg laying continues until late June to mid-July. This appears to be the typical pattern for North American emydines (Risley, 1938; Atland, 1951; Miller, 1959; Moll and Legler, 1971; Christiansen and Moll, 1973; Moll, 1973; Shealy, 1976). Testis size was noted to be greatest in the fall and smaller in the summer. Shealy (1976) found active sperm present in the epididymis of mature male *G. pulchra* throughout the year, suggesting that mating could occur throughout the year in Alabama. Mating is potential in Wisconsin in both fall and spring. Males of all three species cap-

tured in October, November and April courted and attempted copulation when returned to an outside enclosure at the laboratory.

Courtship by laboratory raised males and males caught in the wild was observed in the laboratory (Vogt, 1978), and high speed motion pictures were made to analyze differences among the three species. Males identify conspecific females by both visual and olfactory cues. Specific odors appear to be associated with the cloacal region of females since a male, after placing his nostrils in close proximity of the cloaca of a conspecific females, often swims rapidly to her head and begins courting; however, evidence for long distance pheromones has not been substantiated (Vogt, 1979).

Courtship in *G. ouachitensis* and *G. pseudogeographica* also seems to be initiated by visual cues. Males have been observed to court conspecific females and often other males after orienting towards the head without initial cloacal contact.

Once a turtle is suspected to be a conspecific female, males may immediately try to mount or they may begin courtship. The courtship displays of the three species differ significantly and are probably responsible for maintaining genetic isolation between species pairs.

The aquatic displays of *G. ouachitensis* and *G. pseudogeographica* are remarkably similar. The male approaches the female anteriorly with his forelimbs raised above his head and arched laterally. Only the hindlimbs are used to bring him into position. When nose to nose contact is nearly made, (within 3 mm) the forelimbs are brought down, the venters of the forefeet are rotated laterally and the foreclaws are simultaneously drummed against the ocular region of the female head. The duration of the drumming does not differ significantly between the two species but the frequency does. Jackson and Davis (1972) described this as the "titillation" phase of the courtship behavior in *Pseudemys scripta*. The length of the titillation phase was highly variable in both species of *Graptemys* ranging from 280-750 ms (mean 454) in 23 *G. ouachitensis* and 344-834 ms (mean 470) in 13 *G. pseudogeographica*. The mean number of contacts per bout, however, was different for the two species. The mean number of contacts for *G. pseudogeographica*, 10.3, was nearly twice that of *G. ouachitensis*, 5.2.

In addition *G. pseudogeographica* differs by bobbing its head up and down while *G. ouachitensis* holds its head stationary and vibrates the foreclaws. Mounting is attempted whenever the female is almost motionless and does not seem to be dependent on the number of courtship bouts.

Courtship in *G. geographica* differs in that no vibration of the forelimbs has ever been observed. The male may attempt to mount after cloacal contact. Or, after cloacal contact, the male has been observed swimming to the head of the female and, after making snout to snout contact, bobbing his head rapidly in the vertical plane. This is similar to the courtship behavior of *G. pulchra* (Shealy, 1976).

Mounting is facilitated in all three species by the male hooking the tip of his tail around that of the female to maintain balance and to pull her cloaca into position to allow intromission. Once intromission is achieved the pairs have been observed in coitus from 15 sec to over four hrs. During this time the male remains in a passive state floating at approximately a 45^{o} angle upon the carapace of the female. His forelimbs are usually arched above his head and held motionless.

Reproductive potential

Detailed reproductive data were only

Table 2. Relationship of both carapace length (CL) and average number of eggs per clutch (n = # of clutches measured) and how they relate to size and weight of eggs in *Graptemys pseudogeographica*.

CL	Ave. no. of eggs (n)	Ave. egg length (cm)	Ave. no. eggs (n)	Ave. egg width (cm)	Ave. no. eggs (n)	Ave. clutch wt. (g)	Ave. egg wt. (g)	Ave. no. eggs (n)
17-18	9 (1)	2.78	9 (1)	1.79	9 (1)	53	5.89	9 (1)
18-19	– – –	– – –	– – –	– – –	– – –	– – –	– – –	19 (1)
19-20	9 (1)	3.67	– – –	– – –	– – –	– – –	– – –	9.5 (2)
20-21	12.4 (5)	3.24	11.3 (3)	2.14	12 (1)	117	9.75	11.8 (4)
21-22	14 (2)	3.38	– – –	– – –	17 (1)	147	8.65	13.3 (6)
22-23	14.9 (11)	3.31	14.8 (6)	2.24	12.8 (5)	134	10.5	14.0 (16)
23-24	15.8 (6)	3.45	16 (5)	2.32	13.6 (5)	135 (5)	9.90	14.8 (10)
24-25	14.5 (6)	3.48	14.2 (4)	2.33	14.7 (3)	147 (3)	9.98	15.5 (8)
25-26	16 (1)	3.88	16 (1)	2.47	– – –	– – –	– – –	16 (1)
26-27	22 (1)	3.50	– – –	– – –	– – –	– – –	– – –	22 (1)

Mean 14.1 eggs/clutch

taken from female *G. ouachitensis* and *G. pseudogeographica*. Examination of re- June and July 1972 suggests that females ordinarily lay two clutches of eggs per season. This was determined by presence of two sets of corpora lutea, two sets of corpora lutea and shelled eggs, or one set of corpora lutea and a set of enlarged follicles. However, there was evidence to suggest the possibility of three clutches in eight individuals.

The average clutch size of 50 *G. pseudogeographica* was 14.1 giving an annual reproductive potential of 28.2. Clutches of 65 *G. ouachitensis* averaged 10.5 eggs for an annual reproductive potential of 21. These figures compare with those for *G. pulchra*, 29 (Shealy, 1976) and *G. barbouri*, 17 (Cagle, 1952), both of which are slightly larger in carapace length. As in *G. pulchra* (Shealy, 1976) there was a direct correlation between clutch size and carapace length (Figs. 2 and 3); the longer the female, the greater the number of eggs per clutch. Tables 2 and 3 show the relationship between mean number of eggs and mean egg length, mean egg width, mean egg weight and mean clutch weight at specific carapace lengths for both *G. ouachitensis* and *G. pseudogeographica*. The mean clutch weight and mean egg length increase most noticeably with increase in both female carapace size and clutch size. Average egg weight and egg width are not so strongly correlated. Tables 4 and 5 show the relationship between clutch size and egg weight, length and width. No direct trends or correlations are obvious.

The method of estimating reproductive potential by counting corpora lutea, enlarged ovarian follicles and oviducal eggs has been used in many turtle studies (Cagle, 1952; Moll and Legler, 1971; Christiansen and Moll, 1973; Moll, 1973; Shealy, 1976). Legler (1960) describes the structures in detail. Although this method appears to be realistic, it may lead to overestimation or underestimation of annual reproductive potential. The presence of enlarged follicles toward the end of the laying season must be interpreted with caution. These follicles could represent clutches to be laid the following year, particularly if the individual had nested early the same year.

Table 3. Relationship of both carapace length (CL) and number of eggs per clutch (n = number of clutches measured) and how they relate to size and weight of eggs in *Graptemys ouachitensis*.

CL	Ave. no. of eggs (n)	Ave. egg length (cm)	Ave. no. eggs (n)	Ave. egg width (cm)	Ave. no. eggs (n)	Ave. clutch wt. (g)	Ave. egg wt. (g)	Ave. no. eggs (n)
17-18	11 (1)	3.02	– – –	– – –	8 (1)	74	9.25	9.5 (2)
18-19	9.3 (6)	3.28	9.2 (4)	2.18	8.6 (5)	82	9.54	9.3 (7)
19-20	8.64 (11)	3.46	9.2 (7)	2.16	8.7 (9)	81.8	9.4	8.5 (14)
20-21	10.22 (9)	3.43	9.8 (6)	2.16	9.7 (14)	99.6	10.3	10.1 (19)
21-22	13.4 (9)	3.36	12.6 (8)	2.19	12 (10)	129.2	10.8	12.8 (13)
22-23	12 (2)	3.44	12 (2)	2.24	13.3 (4)	143.8	10.8	13.2 (6)
23-24	11 (2)	3.47	11 (2)	2.12	14.5 (2)	153	10.5	12.3 (3)
24-25	15 (1)	3.59	15 (1)	2.95	– – –	– – –	– – –	15 (1)

Mean 10.5 eggs/clutch

Eight females collected between 8-15 July contained old corpora lutea, oviducal eggs and enlarged follicles. The latest date *Graptemys* was found with oviducal eggs was 28 July, so these enlarged follicles possibly could have ovulated later that same season. One *G. ouachitensis* collected 8 July 1972, contained 12 new corpora lutea, 25 old corpora lutea and enlarged ovarian follicles. Because the average clutch size of *G. ouachitensis* is 10.5 and the record number of eggs per clutch is 17, the 25 old corpora lutea very probably represent two clutches. This female laid three clutches with the potential of laying a fourth.

Between 6 June 1972, and 13 August 1972, 641 mature *G. ouachitensis* and *G. pseudogeographica* were individually marked and released. No turtles were found to contain shelled eggs after they were known to have laid one clutch, but

Table 4. Relationship of clutch size to egg weight, length and width regardless of the carapace size in *G. ouachitensis* (n = number of clutches measured).

Clutch size	Ave. wt./ eggs (g)	n	Ave. length/ eggs (cm)	n	Ave. width/ eggs (cm)	n
6	9.17	3	3.34	2	2.11	2
7	10.00	2	– –	– –	– –	– –
8	9.07	6	3.25	4	2.10	4
9	9.62	11	3.52	14	2.16	11
10	10.77	7	3.08	2	– –	– –
11	12.18	6	3.33	8	2.15	8
13	13.43	3	3.46	1	2.22	1
14	10.64	3	3.40	5	2.21	5
15	9.73	1	3.28	1	2.95	1
16	11.63	2	3.70	1	2.26	1
	479 eggs	47 clutches		39 clutches		34 clutches

since trapping did not start until 6 June, many of the turtles could already have laid their first clutch.

Eggs were obtained from 16 *G. pseudogeographica* and *G. ouachitensis* females which were injected with oxytocin and released between 23 May and 2 June 1977. None of these was recovered during a five day trapping period, 9-14 June 1977 in an attempt to document the laying of more than one clutch in a season. However, two *G. ouachitensis* were observed to have double clutched in 1978.

Twenty-four adult females collected on 15 October 1976, and maintained in the laboratory at 13°C were found to have atretic ovarian follicles upon dissection in January. The livers were distinctly marked with yellow suggesting eggs were being reabsorbed. Atresia has not been observed in freshly caught *Graptemys* during any season. Atresia of small or medium-sized follicles in *Pseudemys scripta* in Panama was reported by Moll and Legler (1971) and by Webb (1961) in Oklahoma. Occurrence of atretic follicles is also known from several other species: *Chrysemys picta* (Powell, 1967), *Terrapene ornata* (Legler, 1960) and *Terrapene carolina* (Atland, 1951). The magnitude of atresia occurring in the 24 *Graptemys* maintained in the laboratory suggests that they are capable of complete atresia of all enlarged follicles if they are under environmental stress.

NESTING

Females emerge from hibernation and begin basking in early- to mid-April. The warmer the temperatures in April and May, the higher the metabolic rate of the turtles; thus the shell may be laid around the eggs more rapidly, allowing the clutch to be laid earlier. This was demonstrated by a female *G. geographica* collected at the Crosby Slough hibernaculum on 5 November and brought into the laboratory and artificially hibernated at 3°-5°C until 10 January. She was gradually brought to 32°C over a 24 hr period. Within 10 days shelled oviducal eggs were present. She was stimulated to oviposi-

Table 5. Relationship of clutch size to egg weight, length and width regardless of the carapace size in *G. pseudogeographica* (n = number of clutches measured).

Clutch size	Ave. wt./ eggs (g)	n	Ave. length/ eggs (cm)	n	Ave. width/ eggs (cm)	n
8	10.0	1	3.47	2	2.24	2
9	5.89	1	3.62	2	1.79	1
10	--	--	--	--	--	--
11	10.0	3	3.24	1	2.09	1
12	10.67	2	3.33	1	2.20	1
13	11.16	2	3.48	6	2.29	2
14	9.64	1	3.33	5	2.20	4
15	9.87	1	3.43	5	2.37	1
16	--	--	3.74	2	2.47	1
17	8.65	1	3.24	1	2.16	1
18	10.0	2	3.44	3	2.28	3
19	9.36	2	3.23	2	2.20	2
	183 eggs	16 clutches		30 clutches		19 clutches

tion by oxytocin injection on 25 January. After 2 months incubation at 25°C the eggs hatched. The onset of nesting appears to be determined by spring temperatures. During the seven years of this study, the earliest first nesting observed was 18 May and the latest 10 June: the last known nesting occurred on 11 July.

Females with shelled oviducal eggs have been found as late as 26 July (1972). Nesting was not observed in 1972 until 9 June, and 95% of the females caught after 10 July did not contain oviducal eggs. This corresponds roughly with the length of laying period in 1977 when the earliest nest was recorded 18 May and laying was nearly finished by 14 June. Temperatures in April and May, 1977, were higher than in the same period in 1972, and may account for the earlier onset of egg laying in 1977 than in 1972 (Table 6). Although the 1977 turtles conceivably could have laid a third clutch in late June or early July, none appeared to have done so since all eggs in the 128 nests examined on 19 August had hatched and only six had young remaining in the cavity.

Map turtles have been found constructing nests from 0545-2030 CST under various weather conditions. The majority of nestings occurred between 0630 and 1000. Later in the day, air and sand temperatures and sun intensity became too great for turtles to leave the water. During overcast days nesting occurred throughout the day. Cool nocturnal air temperatures may also inhibit females from leaving the water to nest. Sixteen females were found on an overcast day at 1400 on Brownsville Island, South Beach in various stages from searching for digging sites to completion of nests. A rain shower at 1430 stopped these activities, and all but one, which was covering her eggs with sand, began moving toward the water. She finished laying before returning to the water. Seven abandoned the nest cavities they had dug.

Table 6

Temperature data (°C) from LaCrosse Weather Bureau (approximately 16 km north of study area)

Month	April		May		June	
Year	1972	1977	1972	1977	1972	1977
Ave. Max.	11.7	19.0	24.6	26.1	26.2	26.0
Ave. Min.	0.6	6.2	10.3	13.2	11.9	14.0
Ave. Temp.	6.1	12.6	17.5	19.7	19.2	20.0

Cloacal temperatures of turtles observed nesting ranged from 24.6°C to 28.2°C; air temperatures ranged from 21.1°C to 32.0°C. During June, from 0430 to 1000 up to 75 females could be seen floating at the surface of the water 3 to 15 m from the shore of nesting beaches. These turtles were apparently waiting for the right combination of environmental cues before emerging. Once a female reached the beach she would wander from 5 to 150 m before attempting to dig a cavity. Nests were located in a variety of settings from the low shrubs surrounding the beach to the open sand area. Usually nests were dug adjacent to clumps of *Carex* or other herbs.

The nest cavities were dug entirely by alternate use of the hind limbs; no body pit such as that I have observed to be prepared by *Chrysemys picta* and *Trionyx spiniferus*, in this area, was dug. The nest cavity is flask-shaped and 10 to 16 cm deep; the neck broadens between four and eight cm beneath the surface. The eggs are positioned and packed into the hole with one of the hind feet. As an egg is being laid the turtle's neck is outstretched fully and the head bobs slightly in the vertical plane. After the last egg is laid, the hole is filled by scraping and packing sand and nearby debris into the hole with the hindlimbs. Once the cavity is filled, the female continues to pack down the nest by alternately raising each hind limb 5 cm above the surface and then

slapping the sand with it.

The female leaves the nesting beach and returns to the water usually through the same break in the vegetation that was used in coming from the water. Fresh nests can be readily distinguished by the striking difference in sand particle size between the nest and the surrounding sand surface. The surrounding sand has a coarse mosaic of small pebbles created by wind erosion of the lighter sand while the nest has a rather uniform small-grained appearance. If found within an hour of nesting, the nest area is moist due to voiding of bladder water and thus darker than the surrounding sand. Nests remain obvious for a week or longer depending on rain and wind erosion. Settling of sand between recently laid eggs and after the eggs hatch forms a shallow crater making the nest even more easily distinguishable. Some of the nesting beaches are so crowded that nests may overlap.

Areas where dredge spoil has been dumped in the last four years are not used for nesting. No plants grow on those sand piles and the water table is too low for the turtles to reach moist sand. Many attempts to excavate nests in dredge spoil banks were noted; digging was apparently abandoned when the cavity failed to hold its form. Abandoned holes were also observed on other nesting areas. Other authorities (Legler, 1960; Shealy, 1976) refer to these as "test holes," implying that the turtle is testing the substrate before laying. This may be the case in some instances, but it is also just as probable that the turtles were disturbed by weather conditions before egg laying commenced, and abandoned the nest. Turtles did not return to complete or lay in these abandoned cavities.

Nest temperatures were monitored continuously from 16 July to 17 August 1972 (Table 7). Thermistors were placed in the center of four nests. Two (a) were 10 cm beneath the surface and two (b) were 14 cm beneath the surface. Two additional thermistors were placed outside of nests: one 1 cm below the sand surface (c), the other 10 cm above the surface in a slatted wooden container shaded by a tree (*Betula*) (d). Daily temperature fluctuations ranged from 2.2 to 12.2°C in the nests. The average daily fluctuations for two nests for 28 days was 6.7°C. The incubation period in nature ranged from 60-75 days (14 nests). Hatching success in nature was approximately 95% in 285 nests, (1972-77) that were excavated after hatching. Hatchlings usually remain in the nest until the yolk is completely absorbed.

Table 7. Nest, substrate and air mean temperatures (°C) from 16 July 1972 to 17 August 1972.

	a Nest, 10 cm below surface	b Nest, 14 cm below surface	c Sand, 1 cm below surface	d Air in shade, 10 cm above surface	e Air, LaCrosse Weather Bureau
Highest high	34.4	31.3	48.9	43.9	35.6
Lowest low	14.4	13.3	8.9	8.9	7.2
Average high	26.1	24.4	36.6	35.0	26.6
Average low	18.8	18.3	14.4	14.4	16.1
Daily mean	22.5	21.4	25.5	24.7	21.4
Daily fluctuations:					
Largest 12.2°C		Lowest 2.2°C			Average 6.7°C

No positive evidence of hatchling overwintering in the nest has been documented for any of the species at this site. Over 500 nests have been examined from mid-September through November without finding young which might yet overwinter before emergence. On 9 June 1972, one hatchling was found crawling across the center of nesting beach no. 5 at 0930 hours. The umbilical scar was dry and crusted and appeared as if the hatchling had not spent the winter underwater. This early sighting is the only evidence suggesting the possibility of occasional overwintering. Overwintering in the nest has been observed for other species *Pseudemys scripta* (Cagle, 1944), *Chrysemys picta* (Hartweg, 1946; Sexton, 1957; Ream, 1967; Vogt, 1978), and *Graptemys* spp (Newman, 1906).

The head and limbs of the hatchlings of all three species are marked similar to those of the adults, but the carapace and plastron tend to be lighter and more boldly marked than in adult. Ontogenetic differentiation and pattern variation among species is discussed elsewhere (Vogt, 1978).

Laboratory incubation

One to two days prior to hatching in the laboratory, droplets of liquid condense on the surface of the egg. The egg by this time has expanded greatly in width and is reduced in length. Within 48 hours one or two longitudinal slits 5 to 20 mm in length appear. Presumably these are cut by the caruncle. These slits increase in length over the next few hours and the hatchling will force its head through the opening. In the laboratory hatchlings will often pull themselves out of the egg with their forelimbs and bury themselves in the substrate. Usually, however, the hatchling will remain in the egg shell for 3-6 days until the yolk sac is nearly absorbed. The caruncle is shed or absorbed within three weeks of hatching.

The temperature at which the eggs are incubated has a dramatic effect on head patterns, scute anomalies, and sex determination. Each of 11 clutches of *G. ouachitensis* and six clutches *G. pseudogeographica* were divided equally between incubators set at 25° and 35°C. Sixty-six eggs were incubated at 25°C, 54 hatched in 66-70 days, six died during development and six did not develop. Seventy eggs were incubated at 35°C, 17 hatched in 49-54 days, 24 died during late stages of development and 29 failed to show any development. The low success at 35°C can be attributed both to temperature and insufficient humidity. The eggs incubated at 35°C often became dented before water was added to the substrate. Five percent of the 60 that developed at 25°C had scute anomalies while 29% of the 41 that incubated at 35°C had them.

Another effect of incubation temperature was the size of the yellow blotches on the head of both *G. pseudogeographica* and *G. ouachitensis*. Ewert (pers comm) noted that postorbital yellow "crescents" were formed in *G. ouachitensis* hatchlings when eggs were incubated at low temperatures (25°C), but not at high temperatures (30°C). He did not notice this effect in *G. pseudogeographica* from Wisconsin. Measurement of the individual area of 13 of the yellow head blotches on hatchlings of both *G. pseudogeographica* and *G. ouachitensis* showed significant differences between eggs of the same clutch incubated at 25°C and 35°C (Vogt, 1978). A greater percentage of larger yellow blotches were formed at the lower temperatures.

Besides the phenotypic effects of incubation temperature, the sex of the hatchling seems to be influenced by incubation temperature. All of those that hatched at

25°C were male and all that hatched at 35°C were female. The probability that 54 of the 66 incubated at 25°C being male as a result of random sampling is very small (< .05 probability in Chi^2 test). Bull and Vogt (1979) showed that sex is environmentally determined under both field and laboratory conditions. Yntema (1976) and Pieau (1971, 1972, 1973) suggested a similar phenomenon for *Chelydra serpentina* and *Emys orbicularis*.

The likelihood of the environmental determination of sex may help to explain the ratio of 5 females per male in the population. The collecting techniques used were sexually unbiased (Vogt, Copeia, in press). Such skewed sex ratios have been reported for other populations of *G. pseudogeographica* (Timken, 1968). He found a 4:1 sex ratio in favor of females in the Missouri River in South Dakota. Hildebrand (1929) found a sex ratio of 4.4 females per male for captive raised *Malaclemys terrapin*. Most other turtle studies have found sex ratios which do not differ significantly from 1:1 (Gibbons, 1970). My observations and collections made of *Graptemys ouachitensis* and *G.p. kohni* in the White River, DeVall's Bluff, Arkansas from 1975-1977 show the opposite trend. About four times as many males as females are seen and caught. Tinkle (pers comm) found the same to be true in Louisiana populations of these species.

The shorter testes can be distinguished at hatchling from the ovaries by the absence of oviducts. Ovaries also have small white spots on the surface. The sex of a turtle apparently is determined prior to hatching, since no sex reversals have been noted from 30 hatchlings maintained in the laboratory for nine months. Hatchlings that were maintained in the laboratory for 5.5 years showed no tendency toward sex reversal once secondary sexual characters became apparent.

Growth in laboratory reared hatchlings

So few yearling and immature turtles were discovered in the study area that hatchlings had to be reared under artificial conditions to answer several questions concerning growth and demographic phenomena, such as: What is the sex ratio at hatching? Is the differential sex ratio in the adult population an index of the sex ratio at hatching or is differential mortality occurring? Do male turtles grow more slowly than females and thus are they more susceptible to predation for a longer period of time, or do male and female turtles grow at equal rates initially, following which males slow in growth upon reaching a specific size (sexual maturity)? When do the external sexually dimorphic characters appear? When is sexual maturity reached?

A total of 197 hatchlings consisting of 65 *G. ouachitensis* from 17 clutches and 132 *G. pseudogeographica* from 19 clutches were reared in the laboratory. At hatching both species were of similar size (Table 8).

Growth of 86 turtles was measured through 10 March 1975, but 47 of these died in the fall of 1975 due to a virulent infection of the bacteria *Citrobacter freundii*. The 39 that survived after treatment with chloromycetin were maintained through 25 October 1978.

During the first three years males and females increased in mass and shell proportions at nearly the same rate (Figs. 4-9). Male growth began tapering off between March 1975 and June 1976, at 3-4 years of age. Females, however, continued growing up to the present.

Table 9 summarizes the change in the mean monthly increment of growth for males and females in 1975 and 1978 and the effect these differences had on total mass and shell measurements. Monthly increase in carapace length of males and

Table 8. Measurements of hatchling *G. ouachitensis* and *G. pseudogeographica* incubated in the laboratory in 1972. (mean above; range below)

Species	*G. ouachitensis*	*G. pseudogeographica*
# of clutches	16	10
# of hatchlings	116	99
Ave. wt. (g)	4.4 g	4.99 g
	(1.5-6.2)	(1.8-6.6)
Carapace length (cm)	3.07	3.04
	(2.71-3.44)	(2.50-3.30)
Carapace width (cm)	3.01	3.04
	(2.65-3.40)	(2.66-3.37)
Plastron length (cm)	2.85	2.84
	(2.53-3.18)	(2.38-3.16)
Plastron width (cm)	1.97	1.96
	(1.75-2.65)	(1.55-2.12)

females was similar through March 1975, 0.50 mm and 0.43 mm respectively. But from March 1977, to April 1978, the average growth per month differed dramatically, 0.56 mm for males and 1.6 mm for females. The average monthly increase in carapace length from November 1972, through March 1975, (27.5 months) was similar to males and females (1.27 mm and 1.38 mm). However, females grew at over twice the rate of males for the next 37 months (March 1975, through April 1978). Carapace length increased an average of 1.06 mm per month in females, but only 0.52 mm per month in males. Reduction in growth rate of males coincided with the onset of sexual maturity. When the males were four years of age they were considered sexually mature on the basis of extensive development of the external secondary sexual characters (elongated 2nd, 3rd, and 4th foreclaws, elongation and thickening of the tail, and courtship and copulation behavior).

By April 1978, none of the 1972 hatchling females had yet reached sexual maturity. This was evident by their being smaller than the smallest mature female found in the wild and possession of no palpable shelled eggs. At least two of the

Table 9. Growth (cm) rates of 1972 hatchlings. *Graptemys pseudogeographica* and *G. ouachitensis* are combined – growth rates were the same.

	10 March 1975				*15 April 1978*			
	Average		Monthly Growth		Average		Monthly Growth	
	53 ♂	33 ♀	53 ♂	33 ♀	20 ♂	19 ♀	20 ♂	19 ♀
CL	6.30	6.87	.50	.43	8.46	11.73	.56	1.6
CW	5.71	6.01			7.04	9.52		
CH	2.68	2.79			3.37	4.87		
PL	5.61	5.80			7.34	10.50		
PW	4.10	4.20			5.12	7.07		
Wt.	35.5	44.5	.96	2.52	85.0	268.4	1.07	7.69

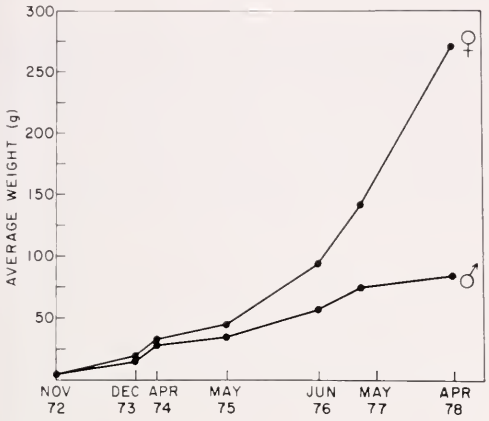

Figure 4. Weight changes in 197 captive raised hatchlings. (65 *G. ouachitensis*; 132 *G. pseudogeographica*).

G. pseudogeographica females will reach reproductive size by spring 1980 if present growth rate continues. Because of the continuous warm temperatures and high intensity light regime under which the turtles were raised and continuous

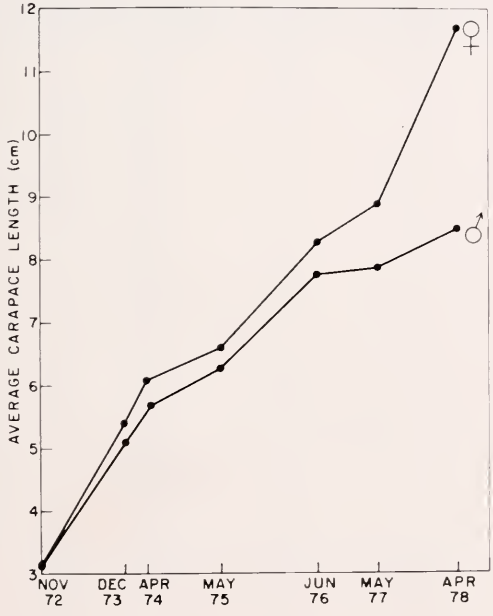

Figure 5. Carapace length changes in captive raised hatchlings.

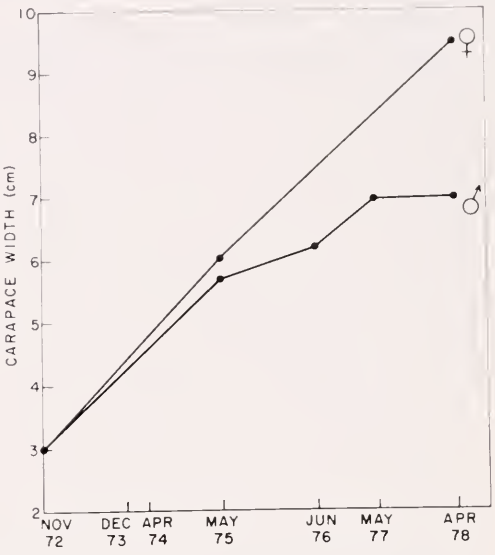

Figure 6. Carapace width changes in captive raised hatchlings.

feeding, these laboratory populations cannot be compared directly to natural ones. However, females did become less active and ate less from January through March each winter when ambient external temperatures reduced the interior vivarium temperatures approximately 7°C.

Growth rings

The use of growth rings to estimate the age of turtles has been reported by nu-

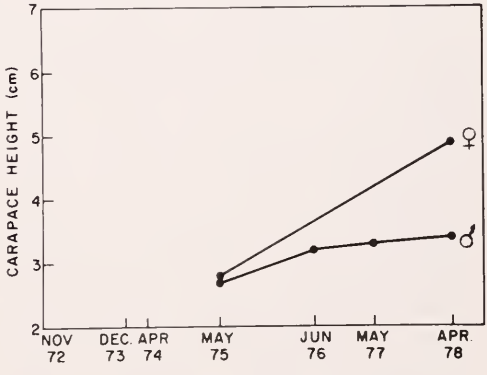

Figure 7. Carapace height changes in captive raised hatchlings.

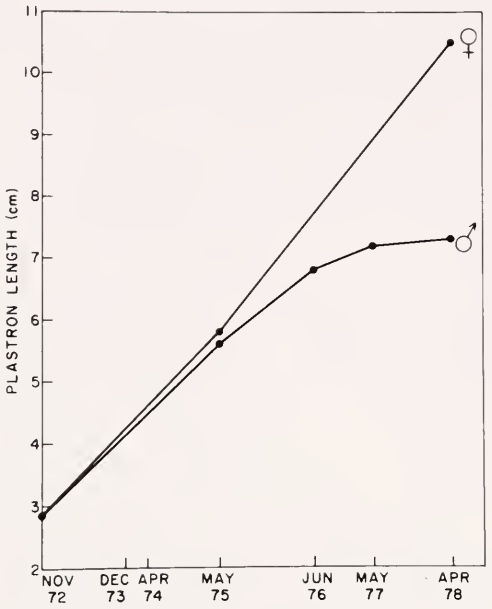

Figure 8. Plastron length changes in captive raised hatchlings.

merous authors (*Graptemys pulchra*, Shealy, 1976; *Terrapene ornata*, Legler, 1960; *Pseudemys scripta*, Cagle, 1946; 1950; Moll and Legler, 1971; *Chrysemys picta*, Sexton, 1959; Gibbons, 1967; Ernst, 1971; *G. ouachitensis*, Webb, 1961; *Pseudemys rubriventris*, Graham, 1971; *Gopherus agassizi*, Patterson and Brattstrom, 1972).

Counting of growth rings gives a rough estimate of the age of the turtle, but can be used reliably only if the areola (hatchling scute) is present. In the Stoddard population of *Graptemys* (all 3 species) the maximum number of rings observed is six in males and up to twelve in females (Table 10). After that time earlier rings become worn off, and growth is so limited that new rings are difficult to distinguish. As the turtles continue to shed epidermal scutes the rings become less and less visible, until the shell is relatively smooth. Thus reliable estimate of the ages of most males over 6 and females over 12 years was impossible. A *Graptemys pseudogeographica* survived 32 years captivity (Bowler, 1977). Cagle (1950) suggested that *Pseudemys scripta elegans* were reproductively active for 40 to 50 years, and that natural longevity extended from 50 to 75 years. Moll and Legler (1971), however, were more conservative, estimating 30 years longevity for tropical *Pseudemys scripta* under natural conditions. Gibbons (1968) estimated some Michigan *Chrysemys picta* to be nearly 40 years old. Judging from the size and age structure of the Stoddard population, and the degree to which shells of some individuals are worn, 30-50 years seems a reasonable estimate for the present age of many individuals.

Natural Growth

The smallest sexually mature male *G. ouachitensis* caught in the wild was 7.48 cm in carapace length. Wild caught *G. geographica*, *G. ouachitensis* and *G. pseudogeographica* males were not reproductively mature in their 3rd year, but did mature in four to six years.

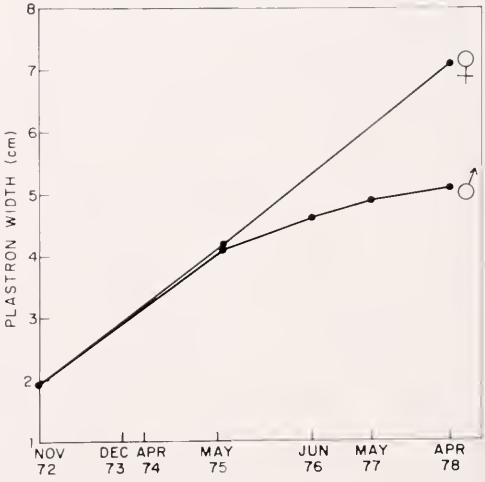

Figure 9. Plastron width changes in captive raised hatchlings.

The youngest mature female *G. ouachitensis* and *G. pseudogeographica*, as evidenced by the presence of shelled eggs, were in their eighth year. Female *G. geographica* that were in their tenth and twelfth years had not yet matured (based on a lack of enlarged ovarian follicles).

Figures 10 and 11 and Table 10 show the relationships between the number of growth rings and the weight and carapace length respectively for *G. ouachitensis* females from the wild. The growth rate pattern of wild females is similar to that shown for captive raised hatchlings (Figs. 4 and 5). The curve (Fig. 10) shows a trend in which carapace length levels off and growth slows. Like the males, females appear to level off in carapace growth once reproductive maturity is reached.

Recapture of nine *G. pseudogeographica* and six *G. ouachitensis* adult females between one and five years after first marking showed very little increase in carapace length, 1.1 mm per year (Table 11). Two individuals decreased slightly in length, which could be due to carapace wear or original measurement error or shrinkage. Ream (1967) also reported loss in carapace length in *Chrysemys picta*. Although increase of the carapace length slows after maturity, 13 individuals exhibited an increase in body weight. The average change in weight for the 15 females (both species) was +49.2 g/yr. Laboratory raised females gained nearly twice as much in body weight in their fifth year of growth, 96.06 g/yr. Changes in carapace cross section to accommodate more eggs continue after ma-

Table 10. Number of growth rings and size of wild caught *G. ouachitensis* ♀ s.

Age	Wt. (g)	CL (cm)	CW (cm)	CH (cm)	PL (cm)	PW (cm)	Maturity
0	4.4	3.1	3.0	1.4	2.9	2.0	hatchling
2	53	7.6	6.5	3.2	6.7	4.5	juv.
3	64	7.8	7.0	3.5	7.3	5.4	juv.
4	170	10.9	9.4	4.6	10.2	6.8	juv.
5	261	12.5	10.2	5.2	11.8	7.5	juv.
6	515	16.6	12.8	6.8	15.8	9.5	juv.
7	441	15.7	12.2	6.2	14.4	9.3	juv.
8	572	16.6	12.6	6.7	15.7	9.4	
8	605	16.5	13.4	6.7	16.2	10.7	
8	767	18.3	14.2	7.4	17.2	11.0	
8	564	16.3	12.8	6.7	15.2	9.3	
8	560	17.2	13.2	6.5	15.4	9.7	
8	557	16.7	13.1	6.2	15.6	9.3	
9	983	20.3	16.1	8.1	19.3	12.2	
9	748	17.8	13.6	7.6	16.6	10.2	eggs
?	1000	16.3					eggs
?	682	17.4					immature
?	555	16.0					immature
10	1031	20.0	15.3	8.0	18.2	11.3	
10	815	19.1	14.1	7.4	17.7	11.1	
11	714	17.4	13.8	7.2	16.1	12.4	eggs
11	1048	21.1	16.5	8.5	19.3	12.0	eggs
12	1032	20.0	15.7	8.4	18.8	11.7	

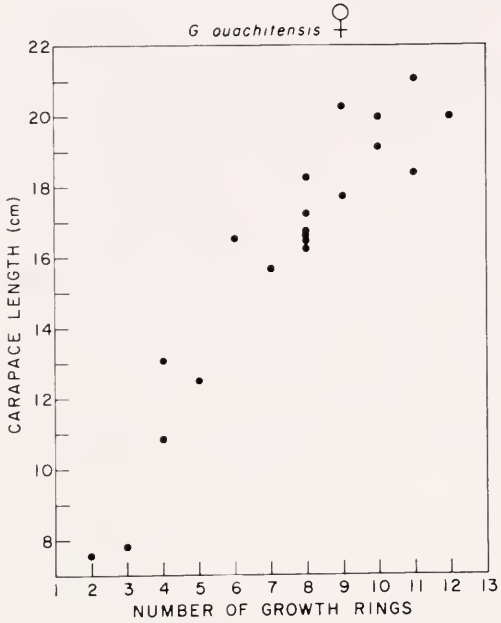

Figure 10. Relationship between carapace length and number of growth rings in wild caught female *G. ouachitensis*.

turity and probably are responsible for the increase in weight. Males show little change in carapace length or shape following maturity.

POPULATION COMPOSITION

Frequencies of size classes of carapace length and weight are shown in Figures 12-15. Definite peaks in both weight and carapace length depict the larger average size of *G. pseudogeographica* females; 82% of the *G. pseudogeographica* females range between 21-25 cm while 85% of the *G. ouachitensis* females range between 19-23 cm. *G. ouachitensis* also weigh less than *G. pseudogeographica* females: 85% of the *G. ouachitensis* were between 800-1400 g while 79% of the *G. pseudogeographica* were in the 1100-1800 g categories. The peak carapace length reached in females probably represents the size at which growth rate decreases at the onset of reproductive maturity. The broader distribution for weight may be due to bias introduced by weighing turtles with full or empty bladders, or with or without mature eggs.

Males of both species are extremely uniform in weight and body size. This reflects the early age of maturity and the slowing of growth after maturity, as was shown in the laboratory population.

POPULATION DYNAMICS

The size of the study area and the mobility of the turtles did not allow a reasonable estimate of population density through traditional mark and recapture techniques. Individual turtles were found to move over 4 km up and down stream within the course of a year, so the use of

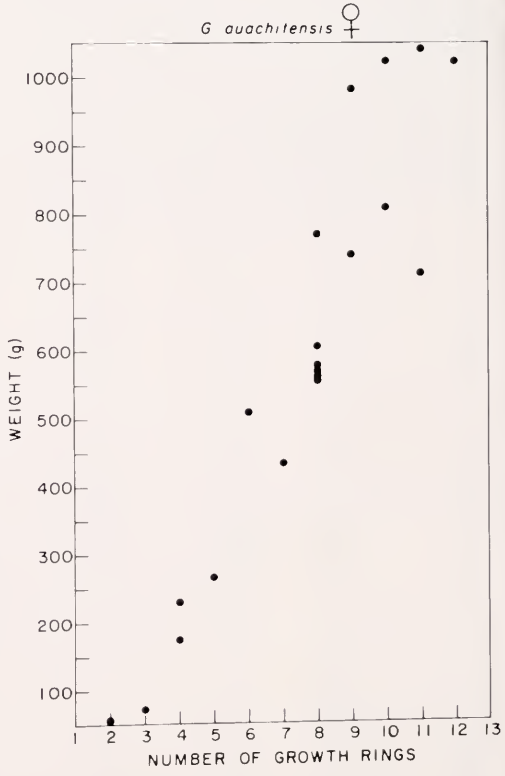

Figure 11. Relationship between weight and number of growth rings in wild caught male *G. ouachitensis*.

traditional mark and recapture index would tend grossly to overestimate the number of turtles actually present. Even in the fall when they are at the overwintering site turtles are moving to different locations (Table 12). This was evidenced by the capture and release of 131 *Graptemys* on 13 October 1977 at the "hibernaculum" in Crosby Slough. On 11 November 1977, 113 *Graptemys* were caught at the same site, but only two of these were turtles that were marked on 13 October.

From 3 June through 13 August 1972, stationary fyke nets were set, and usually checked daily, at 15 localities at Stoddard (Fig. 1). During that period, 326 *G. pseudogeographica* (299 females and 27 males) and 168 *G. ouachitensis* (167 females and one male) were captured.

The highly skewed sex ratio apparent in these totals was biased by extensive trapping adjacent to nesting beaches where females were usually abundant. Traps adjacent to the beaches caught 257 females and only two males. Traps set away from beaches and sloughs, in shallow weedy areas caught 196 females (156 *G. pseudogeographica,* 40 *G. ouachitensis*) and 26 males (25 *G. pseudogeographica,* one *G. ouachitensis*). This was still an overestimate of females since male *G. ouachitensis* were found primarily along the sloughs in moving water. Female *G. ouachitensis* were found primarily in the backwater areas adjacent to islands and

Table 11. Growth of marked turtles in the wild.

#	CL (cm)	△ CL (cm)	△ Wt. (g)	Time after marking
Female *G. pseudogeographica*				
256	22	.9 (.225)	158 (39.5)	4 yr.
342	23.1	.2 (.047)	613 (144.2)	4 yr., 3 mo.
441	23.8	.1 (.044)	152 (67.5)	2 yr., 3 mo.
57	23.1	.4 (.092)	215 (49.88)	4 yr., 4 mo.
59	24.8	2.0 (.4)	412 (82.4)	5 yr.
204	21.0	0	102 (19.4)	5 yr., 4 mo.
331	22.9	.2 (-.041)	425 (86.7)	4 yr., 11 mo.
418	23.1	.7 (.143)	180 (36.7)	4 yr., 11 mo.
594	22.8	1.0 (.02)	58 (11.8)	4 yr., 11 mo.
Male *G. pseudogeographica*				
595			-11	4 yr., 11 mo.
598	15.1	.6 (.12)	+23	5 yr.
602	13.4	.1	+6	4 yr., 11 mo.
Female *G. ouachitensis*				
214	21.8	.8 (.2)	297 (74.25)	4 yr.
685	20.9	.1 (.1)	53 (53)	1 yr.
714	19.2	0	43 (-43)	1 yr.
496	22.1	.3 (.071)	- 15 (-3.53)	4 yr., 3 mo.
47	20.8	1.8 (.45)	250 (62.5)	4 yr.
377	20.6	(-.1)(-.044)	128 (56.8)	2 yr., 3 mo.

CL = carapace length at last capture; △CL = change in carapace length since first capture with average yearly change in parenthesis; △Wt. = change in weight since last capture with average yearly gain in parenthesis

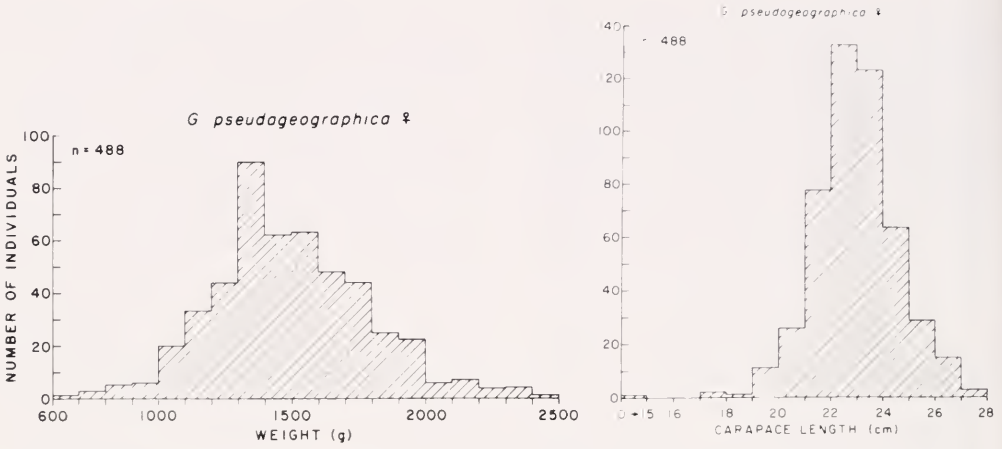

Figure 12. Weight and carapace length classes of *G. pseudogeographica* females captured.

sloughs and were less abundant in shallows away from islands or in moving water.

Gill nets set by commercial fishermen adjacent to the nesting beaches of the main island caught nearly equal numbers of female *G. ouachitensis* (44) and *G. pseudogeographica* (45), but more female *G. pseudogeographica* (142) than *G. ouachitensis* (115) were caught in fyke nets adjacent to the nesting beaches. Female and male *Graptemys ouachitensis* outnumbered *G. pseudogeographica* when trammel nets were set in the sloughs near overwintering sites. In the fall of 1976 and again in 1977, 239 *G. ouachitensis* (191 females and 48 males) and 67 *G. pseudogeographica* (45 females and 22 males) were captured. Since males of both species are found primarily in the

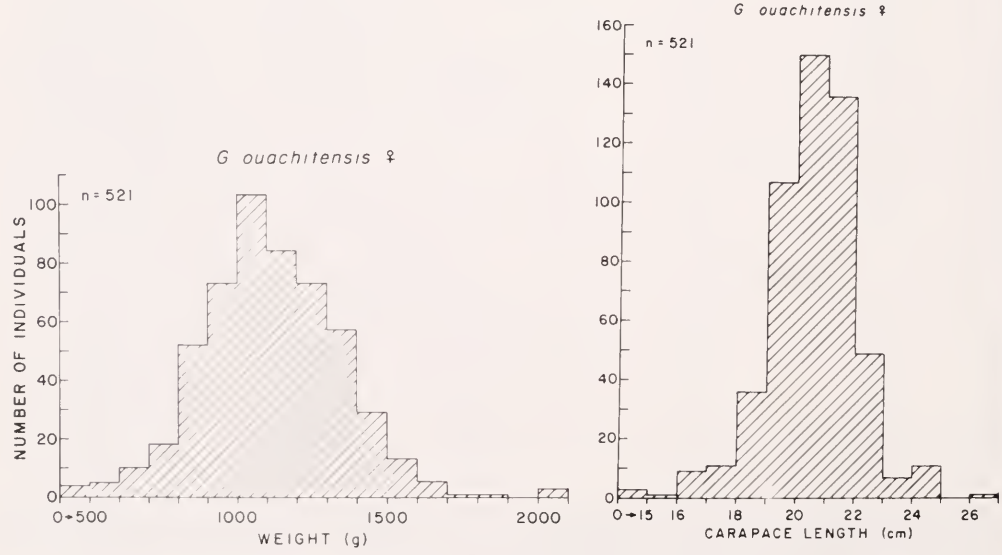

Figure 13. Weight and carapace length classes of *G. ouachitensis* females captured.

Table 12. Turtles caught at Crosby Wing Dam overwintering site.

Date	*G. geographica*			*G. ouachitensis*			*G. pseudogeographica*			Total
	♂	♀	Juv.	♂	♀	Juv.	♂	♀	Juv.	
Oct. 1, 1976	0	4	0	7	49	0	6	19	0	85
Oct. 13, 1977	3	0	0	30	67	1	14	13	1	131
Nov. 11, 1977	9	5	1	11	70	4	1	11	1	113
	12	9	1	48	186	5	22	43	2	329

sloughs and female *G. pseudogeographica* occur primarily in the backwaters, male *G. pseudogeographica* are over-represented in this sample. The ratio of male to female *G. ouachitensis*, 1:4 is fairly realistic but may be an overestimate of the males.

In 1972 a total of 802 *G. ouachitensis* and *G. pseudogeographica* was captured. The sex ratio of 12.6 females per male was biased due to trapping near nesting beaches and use of gill nets. An additional 315 (236 females and 79 males) were captured at intermittent trapping intervals in 1975 and 1977. *Graptemys ouachitensis* and *G. pseudogeographica* make up nearly equal numbers of the 1,117 turtles sampled, 573 and 544 respectively. *Graptemys geographica* were not marked in 1972, but were less abundant, making up less than 10% of the total number of *Graptemys* captured. In 1976 and 1977 this species made up only 7% of the total number caught at the hibernaculum.

Trapping results from 3 June through 13 August 1972 ranged from a daily catch of 106 on bright, warm, sunny days during the height of the nesting season to none on cold, rainy days. Fyke nets were used a total of 45 days, capturing an average of 11 new individuals per day.

Only 48 turtles were recaptured one or more times during the course of the study. Any turtle recaptured the day after

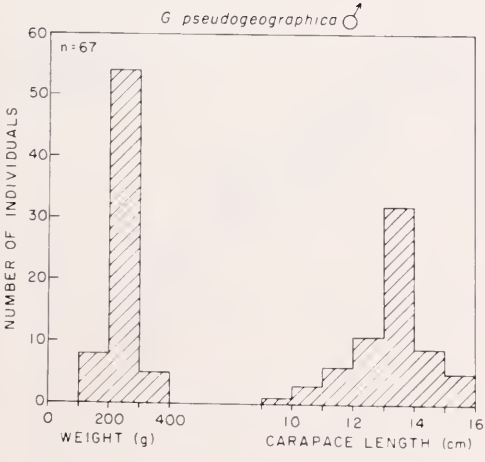

Figure 14. Weight and carapace length classes of *G. pseudogeographica* males.

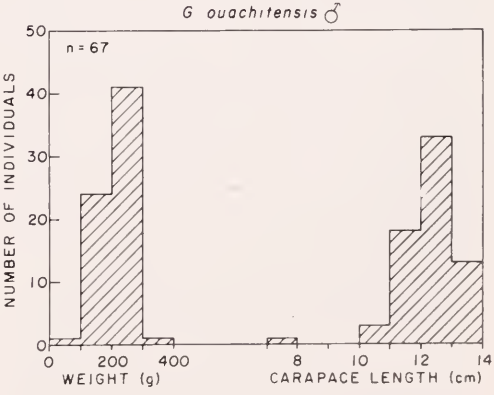

Figure 15. Weight and carapace length classes of *G. ouachitensis* males.

release was not recorded since release was made near the trap site increasing the probability of it being caught in the same trap as it attempted to escape.

MOVEMENTS

During 1972 marked turtles moved distances as far as 4 km. Recapture intervals for females adjacent to nesting beaches ranged from three to 11 days. Since all of these had shelled oviducal eggs upon first capture I assumed that they stayed near the beaches in preparation for laying. Turtles which were caught near the beaches without shelled eggs were never recaptured in the same area in 1972. Twelve were recaptured between 0.4 km and and 1.6 km north of the island from three to 41 days later. Once a female had laid her eggs she vacated the area adjacent to the island and moved into a regular feeding area. Sixteen turtles were recaptured in the same backwater feeding areas 4 to 35 days apart suggesting a regular home range. One female *G. pseudogeographica* first caught after nesting was recaptured three days later 1.6 km north of the island.

Three gravid females caught near the island in 1972 were recaptured near the same beaches in May, 1977. This suggests that an individual turtle may return to the same area to nest year after year. Two females marked near the nesting beaches in June, 1972, were found in October of the same year 4 km north in Crosby Slough in a communal hibernaculum. Nine more recaptures from 1972 were made there in 1976 and 1977. Two turtles hibernating in Crosby Slough in 1976 were recaptured there in fall 1977.

A female *G. pseudogeographica* found on the nesting island 14 June 1976, was released at the boat landing at Stoddard, 15 June 1976. She was recaptured at the Crosby Slough hibernaculum 13 October 1977. This is approximately 8 km from her point of release. Shealy (1976) showed that female *G. pulchra* were capable of homing up to 15 km both up and downstream from points of release to points of original capture, but displaced males tended to be recaptured near the release point. He suggested that this could be because only males have a defined home range. A male *G. pseudogeographica* caught at Crosby Slough wing dam 14 October 1972, was recaptured at the same place 13 October 1977. It had been released at the Stoddard landing in May, 1973, so, like females, males possess homing ability; however, if males regularly travel long distances is not known. The long distances regularly moved by the females from overwintering areas, to nesting grounds, to feeding areas and back to overwintering areas suggests that females have a large irregular activity area defined by the pool itself.

FOOD AND FEEDING

Detailed analysis of food partitioning and feeding behavior is reported in Vogt (1978). The stomach contents taken during June, July, and August from 21 female *G. geographica*, 54 female *G. ouachitensis* and 35 female *G. pseudogeographica* were quantitatively analyzed by volume. Female *Graptemys geographica* were shown to be mollusk specialists, mollusks made up 66% by volume of all their food. Insect larvae and fish carrion comprised most of the remainder. Mollusks were also important in the diet of female *G. pseudogeographica* (19% by volume). In *G. ouachitensis*, however, mollusks made up only 2.8% of the volume.

Vegetation comprised only 3.9% of the volume of material consumed by *G. geographica*, whereas *G. ouachitensis* and *G. pseudogeographica* consumed 31.5% and 42.4% respectively. Algae, *Potamogeton*, *Lemna* and *Vallisneria* were the

plants most frequently eaten.

Insects (caddisfly cases, mayfly larvae, damselfly larvae) comprised 51% by volume of foods eaten by *G. ouachitensis* females; while only 21.9% and 15.3% in *G. pseudogeographica* and *G. geographica* respectively.

No differences in food habits among the males of the three species could be determined. Mayfly larvae, damselfly larvae, caddisfly cases, beetles, flies, other insect larvae, mollusks and fish carrion were eaten by males of all three species but only trace amounts of vegetation were found to have been eaten.

ACTIVITY

Seasonal

Map turtles become active in western Wisconsin in April when they begin dispersing from their overwintering sites while the water temperature is still 4-7°C (Fig. 16). Mating presumably takes place while the turtles are still concentrated around the hibernaculum, but due to water opacity, courtship has never been observed in the wild. I have observed species such as *Emydoidea blandingi*, *Chrysemys picta* and *Chelydra serpentina* mating and courting at this time both north and south of this site in Wisconsin, thus water temperatures are not too cold to allow turtles to breed at this time.

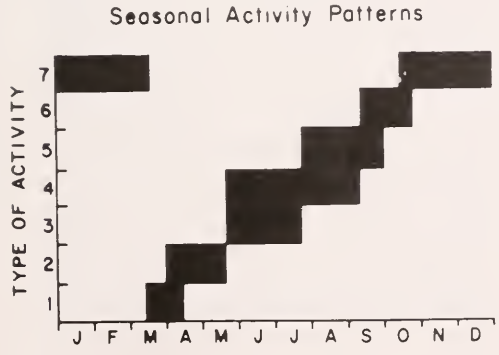

Figure 16. Generalized seasonal activity patterns of *G. ouachitensis* and *G. pseudogeographica*. 1. Emergence from overwintering sites. 2. Dispersal from overwintering sites and basking. 3. Egg laying. 4. Feeding. 5. Hatchling emergence. 6. Backing and movements to overwintering sites. 7. Aggregating at overwintering sites.

During May females move out of the channels and toward the nesting islands. They concentrate to bask by the dozens on the few available emergent logs near the nesting beaches. Male *G. ouachitensis* remain along the channels and sloughs, but during the summer many male *G. geographica* and most male *G. pseudogeographica* move into the quiet backwaters to forage. This is evidenced by the summer fyke net catches in 1972, in which 27 male *G. pseudogeographica* and two male *G. ouachitensis* were captured in the shallow, weedy area, 0.4 - 2.4 km north of the island. Many male *G. geographica* were also caught in this area, but were not marked.

Earliest documented feeding by females occurred on 26 May. There are several possibilities why feeding does not commence until this time: (1) there is not enough room in the body cavity for the stomach or the intestine to expand with food until the first clutch of eggs is laid; (2) the aquatic vegetation and insect larvae on which they feed have not grown to harvestable quantities; or (3) temperatures are not high enough to allow efficient digestion.

All of these ideas are plausible for females of both *G. ouachitensis* and *G. pseudogeographica*, but females of *G. geographica* feed nearly exclusively on mollusks which are abundant throughout the year. They do not consume as large a volume of food as do the other two species, so do not have as great a problem with limited gut space. The earliest *G. geographica* with food in its stomach was located 26 May, only 4 days before the first *G. pseudogeographica* and *G. ouachitensis*. Why feeding is postponed until

such a late date is unclear.

In late May or early June (23 May-10 June) the turtles lay their first clutch of eggs and then move away from the nesting islands to feed for two to three weeks while shell is being deposited around the second clutch of enlarged ovarian follicles. *Graptemys geographica* and *G. pseudogeographica* move far into the backwaters where there are patches of *Potamogeton* and *Vallisneria* and many stumps available for basking. Though some females of *G. ouachitensis* also move into the backwater areas, many stay near the nesting islands to feed and bask or move to the vegetation patches immediately adjacent to the river channel.

After laying their second clutch of eggs the females return to the feeding grounds. Most female *G. ouachitensis* then move away from the nesting islands to the vegetation patches adjacent to the sloughs or channels.

Feeding continues until the first week of September. The turtles then spend the next two months basking, during which time their guts are evacuated presumably so that they can enter hibernation with an empty gut cavity. Turtles which were not allowed to clear the gut cavity before they were artificially hibernated in the laboratory died in 1-2 months, whereas those that were allowed to, lived until Spring.

By October map turtles begin moving to the wing dams along the sloughs and channels. Here they are able to lodge themselves within the rock piles, so not to be carried away by the current and are supplied with a constant flow of well-oxygenated water. They are not totally dormant throughout the winter as commercial fishermen occasionally catch them in their nets while gill netting under the ice. The seasonal activity patterns of *G. ouachitensis* and *G. pseudogeographica* are generalized graphically in Figure 16.

Basking activity

The functions of basking behavior in turtles have been discussed at length by other investigators (Cagle, 1950; Boyer, 1965; Moll and Legler, 1971; Auth, 1975; Shealy, 1976). The primary function of basking is thermoregulatory in nature.

On 14 June 1977, between 1545 and 1550 hours, six female *G. ouachitensis* and one male *G. ouachitensis* were chased from a basking log into a trammel net. The air temperature (sky partially overcast) was 21.5°C and the water, 22.5°C. Cloacal temperatures of the six females ranged from 23.8°C to 27°C (mean 25.8°C); the male was the same temperature as the water – 22.5°C. No other data were obtained on internal temperatures of basking turtles. Since they bask for hours even at ambient temperatures above 35°C, on sunny days their body temperatures must reach considerably higher. Moll and Legler (1971) reported voluntary core temperatures in basking *Pseudemys scripta* as high as 35.7°C. As temperatures approach the critical thermal maximum, basking turtles begin gaping (Moll and Legler, 1971). Male *Graptemys* were observed gaping more frequently than females.

Basking activity was observed between 0900 and 1800. Throughout the day a turtle would alternate between basking, feeding or other activity in the water. Basking sites were at a premium in the study area. Turtles used partially emerged logs, stumps, rock piles, muskrat houses, and sand bars as basking sites. Logs or stumps that were not adjacent to a shoreline were used more frequently than any other type of basking site. Many, particularly males, would often climb onto the highest limbs of a basking log, often 2 m above the water. As turtles climbed onto basking logs they would usually become oriented in an anterior to posterior or posterior to posterior direc-

tion with respect to nearest neighbor. Not only would this reduce the possibility of aggressive interactions by avoiding head to head contact, but also allowed for closer packing on the log by allowing a turtle to crawl partially upon the carapace of another turtle. I did not observe any turtles basking with the plastrons resting over the anterior end of the carapace of another turtle. Up to 47 adult *Graptemys* were observed basking simultaneously on a 6 m log with no aggressive interactions. *Chrysemys picta belli, Trionyx muticus* and *T. spiniferus* were also observed using the same basking logs as the *Graptemys*. Male *T. spiniferus* were observed biting male *Graptemys* that moved into the proximity of the head region on two occasions.

Basking turtles were more prone to disturbance by passing boats within the first 5 min of emergence. The diving of one turtle into the water often triggered the entire log of turtles to slip in. After looking in several directions the turtles would all resume basking within 5 to 10 min. Individuals were noted to remain on a basking log for over 100 min before being disturbed. They occasionally lost their balance and fell into the water, precipitating sudden evacuation of the entire log.

Throughout the time *Graptemys* are basking they are extremely alert to and wary of the slightest disturbance. Approach within 30 meters without disturbing them is difficult unless the observer is snorkeling in the water. Communal basking may be advantageous for the sighting of potential predators and also attracting grackles.

Once a turtle became stationary on a basking log it would stretch out the hindlegs to their fullest extent and spread the webbing between the toes. The neck and forelimbs would also be extended. Presumably this position functions to dry out the skin and increase the surface area exposed to solar radiation. But it also has another purpose; to expose the areas under the limbs where leeches attach. Common grackles (*Quiscalus quiscula*) were observed on 10 June and 14 June removing leeches (*Placobdella parasitica*) from the leg and neck cavities of basking *Graptemys* (Vogt, 1979). The grackles moved along the basking log inspecting each turtle, often walking around inspecting all leg cavities of an individual turtle. The turtles seemed to be oblivious of the grackle, even when the turtle was rocked back and forth on the log by the bird pulling at a particularly tenacious leech. Both male and female turtles allowed grackles to hunt for leeches on their bodies. The only two instances of grackle grooming were on basking logs containing over 20 adult turtles. At what size turtles no longer view the grackle as a potential predator and allow cleaning would be interesting to learn.

Predation

No predation upon basking turtles was noted. Nests and eggs were destroyed by red fox (*Vulpes fulva*), raccoon (*Procyon lotor*), and otter (*Lutra canadensis*). Most (90%) of the nests on beaches 2 and 3 were destroyed within 24 hours after laying. If the nest was not raided within 48 hours it was usually not bothered. During 1977 raccoon predation was responsible for the destruction of over 90% of the nests on both ends of Brownsville Island. No nest predation was observed on the main nesting island in 1976 or 1977. Otters excavated nests and consumed eggs during June, July, and August. Adult map turtles appear to have few potential predators in the study area.

In August, when the hatchlings move to the water, flocks of ring-billed gulls (*Larus delawarensis*), crows (*Corvus brachyrhynchos*), grackles, and red-winged blackbirds (*Agelaius phoenice-*

us), have been observed covering the beaches. On one occasion crows were found excavating a nest where hatchlings were emerging. Redwinged blackbirds and grackles were observed eviscerating hatchlings, leaving only the shells on the beach. Great blue herons (*Ardea herodias*) were also seen walking on the nesting beaches from 0600-0700, when hatchlings were leaving the nest, but no predation was observed. Many turtles are found with the carapace gashed, presumably by outboard motors. Individuals missing one forelimb, two forelimbs, or one hindlimb seemed to be able to function adequately, and were found laying eggs. An adult female *G. ouachitensis* collected in 1972 had recently suffered severe injury to the anterior part of the carapace and had lost half of the mandible. She was recaptured in 1976 still able to function with only half the mandible, and her shell was not completely healed after four years.

SUMMARY

Detailed analysis of the systematics of the false map turtle complex indicates that *Graptemys ouachitensis* and *Graptemys pseudogeographica* are separate species (Vogt, 1978). Natural history data were gathered from populations on the Mississippi River, Vernon County, Wisconsin from 1972 through 1978. Turtles were collected in a 230 hectare area by using fyke nets with leads, gill nets, trammel nets and hand captures. Clutches of eggs were collected from females and incubated in the laboratory under various temperature regimes. Hatchlings were maintained in the laboratory for six years to study differential growth rates of males and females, and to determine the time at reproductive maturity and the sex ratios at hatching.

Examination of reproductive tracts of 50 females suggests that they annually lay two clutches of eggs. Eight females perhaps laid three clutches. The average clutch size of 40 *G. pseudogeographica* was 14.1 and for 65 *G. ouachitensis* was 10.2. There is a direct correlation between clutch size and female carapace length. The mean clutch weight and mean egg length increase with an increase in female carapace length and also the clutch size.

Females begin developing enlarged ovarian follicles in mid-July and enter hibernation with the body cavity packed with enlarged follicles in October (Fig. 16 shows the occurrence of major seasonal activity patterns). Mating probably occurs either in October or April while the turtles are congregated around hibernacula.

The courtship displays of male *G. ouachitensis* and *G. pseudogeographica* involve drumming of the foreclaws against the ocular region of the female. There was a mean of 10.3 (n = 26) contacts per "titillation" bout for *G. pseudogeographica* and only 5.2 (n = 24) for *G. ouachitensis*. *Graptemys pseudogeographica* also differs by bobbing its head in a vertical plane while *G. ouachitensis* holds its head stationary while vibrating the foreclaws.

Fresh nests were found from 18 May to 11 July, but females with shelled oviducal eggs were found as late as 26 July. However, 95% of females captured after 10 July lacked oviducal eggs.

Nest temperatures, monitored continuously from 16 July to 17 August 1972, fluctuated from 2.2°C to 12.2°C daily. The mean daily fluctuation for two nests for 28 days was 6.7°C. Natural incubation periods ranged from 60-75 days. Hatching success is approximately 95% in both laboratory and nature.

Incubation temperature in the laboratory was shown to affect hatching success, number of scute anomalies, size of yellow blotches on the head, and sex determina-

tion in both *G. ouachitensis* and *G. pseudogeographica*. More scute anomalies occurred at 35°C than 25°C. The yellow blotches on the head were larger on siblings incubated at 25°C than on those at 35°C. All eggs that hatched at 25°C (54 of 66) were male. All eggs that hatched at 35°C (n = 17) were female. These results strongly suggest that, at least in the laboratory, sex can be determined by early developmental temperatures. A sex ratio of 5 females per male was calculated from trapping results. Sex determination by developmental temperature may help to explain the skewed sex ratio in both *G. ouachitensis* and *G. pseudogeographica*.

Sixty-five *G. ouachitensis* and 132 *G. pseudogeographica* hatchlings from 1972 were raised in the laboratory. During the first three years male and females (n = 86) increased at nearly the same rate in mass and shell proportions. Male growth slowed between March 1975 and June 1976 while females continued to grow at the initial rate. Males attained sexual maturity in their fourth year, as evidenced by secondary sexual characteristics, and the slowing of their growth rate is apparently correlated with this. Wild male *Graptemys* of all three species were mature when four to six years old.

No females had matured sexually by April 1978. The youngest wild-caught mature female *G. ouachitensis* and *G. pseudogeographica* were in their eighth year. Growth rings were used reliably to estimate age only during the first six years in males and up to 12 years in females. Mature male and female *G. pseudogeographica* and *G. ouachitensis* recaptured after one to five years showed little increase in carapace length (less than 1.1 mm per year).

In 1972 a total of 802 *G. ouachitensis* and *G. pseudogeographica* were captured. Both male and female *G. pseudogeographica* are able to return to their site of original capture after being displaced downstream as far as 8 km. The long distances regularly moved by females from hibernating sites to nesting grounds, to feeding areas and back to hibernating sites precludes the use of the term home range.

Stomach contents of 21 *G. geographica*, 54 *G. ouachitensis* and 35 *G. pseudogeographica* females were quantitatively analyzed by both volume and frequency of occurrence. *Graptemys geographica* is a mollusk specialist, mollusks composed 66% of the volume of food consumed. Mollusks are also important in the diet of *G. pseudogeographica* females (19% by volume), but they make up only 2.8% of the diet of *G. ouachitensis*. Vegetation makes up a large proportion of the diet of *G. ouachitensis* (31.5%) and *G. pseudogeographica* (42.4%). Insects composed 51% of the volume of food eaten by *G. ouachitensis* while only 21.9% and 15.3% in *G. pseudogeographica* and *G. geographica* respectively.

No differences in food habits were noted among the males of the three species. All consumed insect larvae, mollusks and fish carrion. Female *G. ouachitensis* were observed to be primarily surface feeders. *Graptemys geographica* and *G. pseudogeographica* feed mostly underwater. Map turtles become active in April and begin dispersing from the hibernacula while water temperatures are 4°-7°C. During May females move out of the channels toward nesting beaches where they congregate to bask, but have not been observed feeding until 26 May; presumably they do not feed until after laying their first clutch of the year.

In late May or early June map turtles lay their first clutch of eggs and then move away from the nesting islands to feed for two or three weeks while shells are being deposited around their second clutch of eggs. Feeding continues until

the first week of September. By October all three species are moving toward communal overwintering sites. Up to 131 *Graptemys* have been caught in 30 minutes behind a wing dam in October.

Basking activity was observed primarily between 0900 and 1800 hrs. Throughout the day turtles alternate between basking, feeding or other activity in the water. Basking sites are used communally. Up to 47 adult *Graptemys* were observed basking simultaneously on a 6 m log. No aggressive interactions were observed between basking *Graptemys*. On two different occasions a common grackle *Quiscalus quiscula* removed leeches (*Placobdella parasitica*) from basking *Graptemys*.

Nest predation by red fox, raccoon and otter was observed. Hatchlings were consumed as they emerged from the nest by ring-billed gulls, crows, grackles and red-winged blackbirds. Outside of man, adult map turtles have few potential predators in the study area.

ACKNOWLEDGEMENTS

This study was conducted under the supervision of Dr. William G. Reeder, who supplied field equipment, laboratory space, museum funds and technical criticism of the paper. Drs. Jack P. Hailman, C.J. McCoy, John Neess, M. Ewert and Ms. Marsha Christianson are thanked for their critical comments on the paper's composition. Dr. John Legler and Dr. Michael Ewert are appreciated for providing me access to new techniques and data prior to publication.

Cheryl Hughes is remembered for drawing all of the graphs. Mike Nee helped with the identification of plant species in the study area. Partial support for this study was provided by various travel grants: University of Wisconsin-Madison, Zoology Department Jefferson Davis Fund; University of Wisconsin-Madison Zoological Museum; Carnegie Museum of Natural History-Pittsburgh. Data for part of this study were collected while I was conducting research for the Wisconsin Department of Natural Resources, Bureau of Research. The DNR personnel were instrumental by lending of fyke nets and providing permits to conduct my research.

Throughout this study many students and friends gave freely of their time to help me with some aspect of the study – to all of them I express my sincerest gratitude. Several of them gave up their summers and worked for next to nothing both in the field and in the laboratory. Without their help this study would still be incomplete. To each of them I offer my deepest appreciation: Marsha Christianson, George Dmytrenko, Janis I. Dzelzkalns, D.D. Flambeau Von Rex, Bruce Hellmich, Jeremy Jacobs, Alan Jaslow, Kristine Klevickis, Lisa Mattick, Michael Pappas and Dan Peterson. Robert Peterson made the laboratory part of this study possible. Without his contribution to the care of the hatchling turtles, monitoring of incubating eggs, care of the experimental turtles for seven years, and maintenance of my laboratory facilities a reduced study would have had to be undertaken.

My gratitude is extended most sincerely to Jack Roberts for his assistance and guidance on the Mississippi River at Stoddard. He gave freely of his knowledge of the river, saved turtles captured in conjunction with his commercial fishing operation and provided companionship and local history of the study area. Marsha Christianson provided much needed help in the field and laboratory and prevailed through many trying moments in the editing of this paper. Her patience and understanding will long be remembered. I must also express my thanks to the other occupants of the Birge

Hall Animal House for enduring floods and odors from the turtle growing room and my continual expansion. Carmelita Bell is thanked for typing the final version of the manuscript.

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May 26, 1980

A TAXONOMIC STUDY OF THE COOTER TURTLES, *PSEUDEMYS FLORIDANA* (LECONTE) AND *PSEUDEMYS CONCINNA* (LECONTE), IN THE LOWER RED RIVER, ATCHAFALAYA RIVER, AND MISSISSIPPI RIVER BASINS

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ABSTRACT

The taxonomy of the cooter turtles, *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) was studied in southwestern Louisiana to determine the relationship between these two turtles and to examine the validity of the taxonomic characters currently utilized.

One hundred and sixty-two turtles were examined from the lower Red River, the Atchafalaya River, and the Mississippi River basins. The color patterns and osteological characteristics were numerically scored. A discriminant analysis based on the characters of plastral pattern, carapace pattern, bridge markings, and the number of phalanges in the fifth toes of the hind feet, was conducted on these specimens. Two *a priori* groups of specimens with relatively "pure" characters were selected, one with *P. floridana* characters and one with *P. concinna* characters. From these *a priori* groups a set of discriminant coefficients was calculated for each character and all specimens were assigned Z-values based on these characters.

A linear plot of the Z-values showed most specimens in the sample were intermediate, with Z-values distributed between and overlapping both *a priori* groups. The four characters used had little or no taxonomic value in separating these turtles. The wide range of Z-values found within individual clutches indicated interbreeding of specimens with widely varying characteristics. Correlation coefficients for toe phalanx number and plastral pattern versus carapace length indicated these characters to be ontogenetic.

The results show that *Pseudemys floridana* and *Pseudemys concinna* should be synonymized under the senior synonym, *Pseudemys floridana*, pending discernment of quantitative characters that will distinguish *floridana* and *concinna* as species.

INTRODUCTION

The North American emydid turtles of the genus *Pseudemys* have had a long, confused taxonomic history. Relationships among many of the species complexes are neither understood nor agreed upon. *Pseudemys floridana* (LeConte) and *Pseudemys concinna* (LeConte) are members of one such complex. A taxonomic study of these two species was conducted in the lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana (Fig. 1). The three subspecies reported to occur in this area according to Ernst and Barbour (1972), and Conant (1975) are *Pseudemys floridana hoyi* (Agassiz), *Pseudemys concinna hieroglyphica* (Holbrook), and *Pseudemys concinna mobilensis* (Holbrook). The purpose of this study was to determine the relationship between *Pseudemys floridana* and *Pseudemys concinna* in

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southern Louisiana and to examine the validity of the taxonomic characters currently being utilized to separate them.

Pseudemys concinna ranges throughout much of the southeastern United States and contains the subspecies *concinna, suwanniensis, mobilensis, texana* and *hieroglyphica. P. floridana* occurs in approximately the same geographic range and contains the subspecies *floridana, peninsularis*, and *hoyi* (Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975). According to Ernst and Barbour (1972) *Pseudemys concinna* is an inland turtle that inhabits mainly rivers, preferring those with moderate currents, abundant aquatic vegetations, and rocky bottoms. It occurs, however, in almost any aquatic habitat such as lakes, ponds, swamps, tidal marshes, oxbows, and ditches. *P. floridana* inhabits any aquatic habitat in the coastal plains, preferring those with slow currents, soft bottoms, and abundant aquatic plants.

Figure 1. Study area which includes the Lower Red River, the Atchafalaya River, and the Mississippi River basins in Louisiana.

Taxonomic history. – The species were first described by LeConte (1830) as *Testudo floridana* and *Testudo concinna.* The early taxonomic literature (Bonaparte, 1831; Gray, 1831, 1855, 1863; Duméril and Bibron, 1835; Holbrook, 1836, 1838; Agassiz, 1857; Baur, 1893) involved primarily generic name changes and the addition of new subspecies.

Carr (1935) considered *Pseudemys floridana* and *P. concinna* to be northern and southern representatives of the same species. In LeConte's original description *P. floridana* had page priority so he selected it as the name of the species. Carr (1937) synonymized *P. mobilensis* with *P. floridana* and named a new subspecies *P.f. suwanniensis.* Stejneger (1938) recognized a new subspecies, *P.c. hoyi*, for the specimens which Agassiz had called *Ptychemys hoyi.*

Carr (1938) described *P.f. peninsularis* from Florida and included an analysis and key to the *P. floridana* group. He stated, "Due to inherent genetic instability, or to re-establishment of intercourse between previously isolated stocks, individual variation within a local population (even in a single litter) may result in phenotypes superficially more dissimilar than the actual races." He thought many descriptions stressed characters that were highly variable or sexually dimorphic and that because of this the original descriptions were inadequate. He described the *P. floridana* group as " . . . a *Rassenkreis* which extends westward in two limbs from the Atlantic coastal *floridana* – an inland series (*concinna, hieroglyphica, texana*), and another in the coastal plain (*peninsularis, suwanniensis, mobilensis*)." Carr (1952) redescribed the group and added *P.f. hoyi.*

Crenshaw (1955), in his study of the Florida races *P.f. floridana, P.f. peninsularis,* and *P.f. suwanniensis*, stated that

the relationships between all turtles of this complex were best shown by subdividing the complex into two species, *P. concinna* and *P. floridana*. The species *P. concinna* included the subspecies, *concinna, mobilensis, hieroglyphica, suwanniensis,* and *texana.* The species *P. floridana* included the subspecies *floridana, peninsularis,* and *hoyi.* The present status of these turtles is that suggested by Crenshaw (1955). Many authors include these turtles in the genus *Chrysemys* (McDowell, 1964; Weaver and Rose, 1967), however this has never been uniformly accepted (Holman, 1977) and data presented by Vogt and McCoy (1979) suggest that they should be placed in the genus *Pseudemys* and separated from *Chrysemys.*

Locality records and status. – Specimens of *P. floridana* are not easily distinguished from specimens of *P. concinna* on the basis of presently utilized taxonomic characters. Reported records for the three Louisiana subspecies show that many authors are unsure of the identity of specimens and unwilling to commit themselves as to the exact ranges for each subspecies. One aspect of the problem is the paucity of specimens. Another is the wide range of characters these turtles possess and the wide geographic range they occupy.

Three subspecies occur in Texas according to Brown (1950): *P.f. hoyi, P.c. texana*, and *P.c. mobilensis.* Brown referred to all as subspecies of *Pseudemys floridana*. He noted that the distribution of *P.c. texana* was unclear and that a number of specimens from Bastrop County might prove to be intergrades with *P.f. hoyi.*

Webb (1970) listed *Pseudemys f. hoyi* as occurring in eastern Oklahoma and remarked that *P.c. heiroglyphica* probably also ranged into eastern Oklahoma where the two "occasionally hybridize."

Two subspecies are reported from Arkansas, *C.c. hieroglyphica* and *C.f. hoyi* (Conant, 1975). Michael Plummer (pers. comm. November 17, 1976) has advised me that *P. concinna* appears to predominate in Arkansas populations but that most specimens appear to have intermediate characters.

The subspecies *C.c. hieroglyphica* and *C.f. hoyi* occur in the southern third of the state of Missouri where they hybridize in nature (Anderson, 1965).

Smith (1961) treated all Illinois specimens as hybrids of *P.c. concinna* x *P.f. hoyi.* His remarks included an opinion from Crenshaw which suggested that all southern Illinois turtles be regarded as hybrids because of introgression of *P. floridana* genes into the *P. concinna* populations of the lower Mississippi River Valley. Crenshaw believed this produced an intermediate form.

Two subspecies, *C.c. hieroglyphica* and *C.f. hoyi*, occur in Kentucky (Barbour, 1971). The ranges of these turtles in Kentucky appear to be sympatric and Barbour commented that the two hybridize freely with each other. Barbour (1971) and Conant (1975) showed *C.c. hieroglyphica* and *C.f. hoyi* as occurring in approximately the same ranges in Tennessee.

Three subspecies of *C. concinna* occur in Alabama; they include *C.c. concinna, C.c. hieroglyphica*, and *C.c. mobilensis* (Conant, 1975). One subspecies of *C. floridana, C.f. floridana*, occurs in Alabama (Conant, 1975; Mount, 1976). In dealing with the subspecies of *P. concinna*, Mount (1976) stated that, " . . . the geographic variation was found to be inconsistent with previous reports and assumptions" and nearly all characters used to distinguish the subspecies had wide areas of overlap. He felt the designation of subspecies was largely arbitrary. He chose to allocate all *P. concinna* in Alabama to the subspecies *P.c. concinna* and

noted that hybridization between *P. concinna* and *P. floridana* occurs frequently in the southeastern portion of the state.

Existing records for these turtles in Louisiana (Viosca, 1923, 1926; Cagle and Chaney, 1950) do not give a good indication of the species and subspecies which are found in various localities. Liner (1954) listed three Tulane specimens (TU-1104, 11046, 13618) as *P. floridana*. The first is from Vermilion Parish and the last two are from Terrebonne Parish. These specimens were examined and the data included in my statistical analysis of specimens.

Keiser and Wilson (1969) reported three subspecies of these turtles, *C.c. hieroglyphica*, *C.c. mobilensis*, and *C.f. hoyi*, from Louisiana, Keiser (1976) referred to the two species as the *Chrysemys floridana-concinna* complex and used the presence of a plastral pattern and the C-shaped mark on the second costal scutes of the carapace of *C. concinna* to separate the species. He also mentioned possible skeletal characters separating them, but noted that few Atchafalaya Basin specimens fit the descriptions of the subspecies given by Carr (1952). The localities and specimens cited by Keiser (1976) are included in this study as they constitute the core of the data from which the present study grew.

MATERIALS AND METHODS

Specimens examined. – The specimens used in this study were collected primarily from the Atchafalaya River Basin from 1975 to 1977. Specimens from the Red River and Mississippi River basins were borrowed from the Tulane University collection of amphibians and reptiles (TU). Atchafalaya River Basin specimens are from the University of Southwestern Louisiana collection of amphibians and repitles (USL). A total of 162 specimens was rexamined. All specimens collected during the course of this study were catalogued into the USL collection (Appendix I).

Method of collection. – Several types of traps (Legler, 1960) were used in the collection of adult turtles. Fish, chicken, cottonseed cakes, lettuce, and watermelon were tried as bait. Although no adult *P. floridana* or *P. concinna* were caught, adults of *P. scripta*, and *C. picta* were caught in traps. Most observations of feeding suggest that *P. floridana* and *P. concinna* are primarily vegetarian as adults (Allen, 1938; Carr, 1952; Ernst and Barbour, 1972). The abundance of natural plant foods may account for my inability to trap adult specimens even when plant materials were used as bait.

I obtained adult specimens by purchasing them from fishermen or by searching for nesting females along roads. Road collecting was most successful in the early morning from 5:00 to 8:00 A.M. (C.S.T.) and in late afternoon from 3:30 P.M. until dusk. Five adults from which I later obtained egg clutches were collected in this manner. A gill net was occasionally used in the collection of adult turtles, though with limited success.

Two methods used without success for the collection of juvenile turtles were night collecting and snorkeling. The most successful method of obtaining small turtles was to dip-net basking animals from a canoe or powerboat. Collection methods used in other areas with clear water (Chaney and Smith, 1950) did not work well in central Louisiana. The waters frequented by these turtles in central Louisiana usually are over 1 m deep and are often very turbid.

All eggs were collected from gravid females using Cagle's (1944) method. Specimens were pithed and the entire oviducts were removed. The eggs were removed from the oviducts and placed in an in-

cubator. Five clutches were incubated using Trotter's (1973) technique, with hatching success varying from 5% to 88%. Each clutch of hatchlings was kept alive for several months for observation and to allow color patterns to become distinct.

Osteological preparations. – Phalanges of the fifth toes of the hind feet were examined by X-ray (adult specimens) or clearing and staining (hatchlings and juveniles). The clearing and staining procedure was, with modifications, that of Hardaway and Williams (1975).

Description of taxonomic characters. – A number of taxonomic characters are presently used to differentiate subspecies of *P. floridana* and *P. concinna* in various parts of their ranges. They do not apply to all the subspecies and the reliability of each character varies depending on the subspecies and the locality. As many characters as possible were examined to determine which could possibly be used to separate *P. floridana* and *P. concinna* in the area studied.

Two characters used in this study and referred to in most present taxonomic literature (Carr, 1952; Crenshaw, 1955; Ernst and Barbour, 1972; Conant, 1975) are the plastral pattern and the carapace markings. *P. concinna* is reported to have a C-shaped yellow line on the second costal scute of the carapace (Fig. 2) and a plastral pattern that generally follows the seams of the plastral scutes (Fig. 3). *P. floridana* has either a straight line or an inverted Y-shaped line on the second costal scute of the carapace (Fig. 2) and an immaculate plastron (Fig. 3). Both of these characters are presently used as the major taxonomic characters separating these species. Both are based on pigmentation which, if used alone, is not a reliable taxonomic character at the species level. Variation in color and in the arrangement of pattern can result from non-genetic factors. Temperature may play an important role in pattern determinations especially during embryonic development (Fowler, 1970; Vinegar, 1973, 1974).

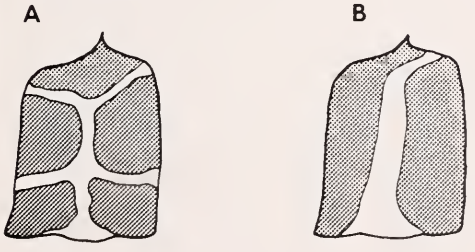

Figure 2. Pattern on the second costal scutes of the carapace; A. C-shaped pattern of *Pseudemys concinna*; B. Straight line pattern of *P. floridana*.

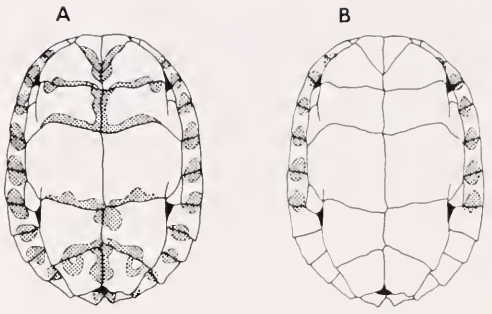

Figure 3. Typical plastral patterns; A. *Pseudemys concinna;* B. *P. floridana.*

Three characters that are used to distinguish various subspecies of *P. floridana* and *P. concinna* are neck stripe pattern, jaw serration, and the pattern on the ventral surface of the marginal scutes. All specimens in my sample were scored for each of these characters. These characters are, however, probably too qualitative and their range of variation too great to be useful in statistical analyses.

The pattern of stripes on the dorsal surface of the neck is used to distinguish *P.f. peninsularis* from *P.c. suwanniensis* in Florida. *P.f. peninsularis* has a hairpin

pattern while *P.c. suwanniensis* has a series of straight lines (Fig. 4). Sample specimens were scored as continuously lined (C), discontinuously lined (D), or hairpin patterned (H), for right and left sides of the neck. Many specimens possessed different combinations of these three categories and some possessed intermediate pattern types.

Jaw serration is used to distinguish *P.c. texana* from the other subspecies of *P. concinna* and *P. floridana*. This character can also be used to distinguish three Florida turtles, *P.f. peninsularis, P.c. suwanniensis,* and *P. nelsoni*, from each other. The sample specimens were scored on the basis of whether their jaws were serrated (S) or unserrated (U) and whether the upper jaw was notched (N) or un-notched (no symbol). The range of variation included that which was found in the above mentioned species long with other variations (Fig. 5).

The pattern on the ventral surface of the marginal scutes is used to distinguish *P. concinna* subspecies from *P. floridana* subspecies in Florida. *P. floridana* reportedly has few or no marginal markings while *P. concinna* may possess a variety of

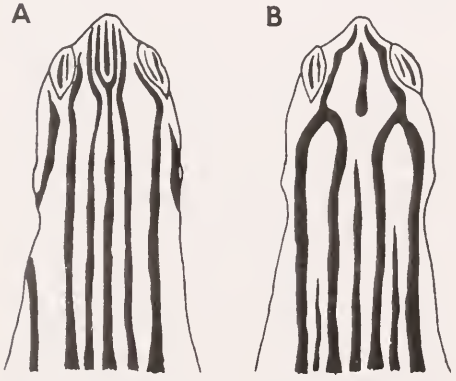

Figure 4. Neck stripe patterns; A. *Pseudemys concinna suwanniensis*; B. *P. floridana peninsularis.*

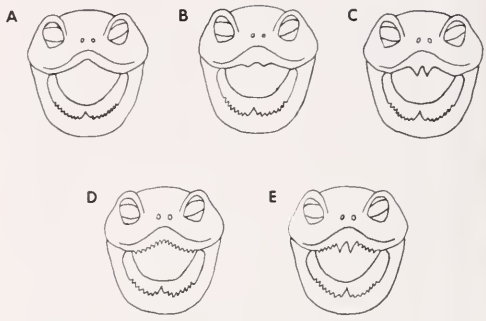

Figure 5. Jaw serrations found in various species and subspecies of *Pseudemys*; A. *P. concinna concinna*; B. *P. floridana hoyi*; C. *P. concinna texana*; D. a Louisiana variation; E. *P. nelsoni* (also found in some Louisiana specimens).

patterns (Fig. 6). Three predominant patterns occurred in the sample, but a fourth type, the absence of markings, was not observed. Patterns were scored as types one to four (Fig. 6).

A character I have analyzed in detail is the number of phalanges of the fifth toes of the hind feet (Weaver and Rose, 1967). Associated with this is the fusion or separation of the astragalus and calcaneum in the ankle (pers. comm. June 17, 1976, with unpublished manuscript attached from Francis L. Rose). These characters, when first used by Weaver and Rose (1967) in their study of the genus *Chrysemys*, appeared to be different for *P. floridana* and *P. concinna*. *P. floridana* reportedly had two toe phalanges and a fused astragalus and calcaneum. *P. concinna* reportedly had three toe phalanges and a separated astragulus and calcaneum (Fig. 7). These differences were theorized to be related to the degree of terrestrial or aquatic habits of each species (unpublished manuscript from Francis L. Rose). *P. floridana*, the more terrestrial turtle, has a shorter fifth toe and a more solid foot for better support while walking on land. *P. concinna* has a longer fifth toe which allows increased webbing; the separate astragalus and calcaneum al-

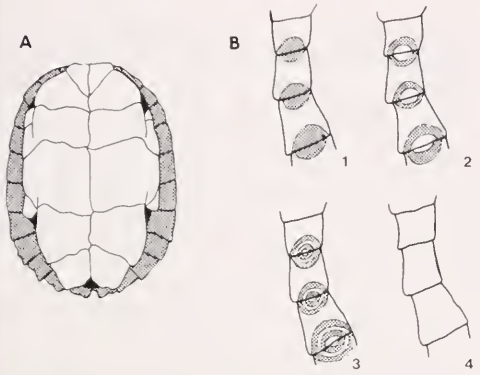

Figure 6. A. Locations of the pattern on the ventral surfaces of the marginal scutes. B. Pattern types found on the ventral surfaces of the marginals and the numerical scoring used to classify these.

so make its foot more flexible for swimming. Rose (pers. comm. October 11, 1976) has states that these characters may or may not be good taxonomic characters.

Penial morphology of *P. floridana* and *P. concinna* was shown to be identical with that of *P. scripta* and *P. nelsoni* (Zug, 1966). Osteological characteristics of the skulls of emydid turtles were analyzed and used for taxonomic purposes by McDowell (1964). He drew a distinction between a *rubriventris* series and a *floridana* series but did not identify any differences between *P. floridana* and *P. concinna*. Skull osteology and penial morphology were not examined in this study.

The precopulatory behavior reported for *P. floridana* (Cagle, 1950) appears to be similar to that reported for *P. concinna* (Marchand, 1944; C.G. Jackson, 1972). If there are subtle behavioral differences between *P. concinna* and *P. floridana* they have not been reported.

Statistical methods. – Markings from the following body and shell regions were recorded for each specimen: carapace, plastron, neck, bridge, and marginal scutes. Toe phalanx number on the fifth toes of the hind feet, fusion of the astragalus to calcaneum, jaw serration, and carapace length were also recorded. The color pattern data were qualitative and various systems of scoring patterns were devised for quantifying these data. The scoring systems used in this study were based on the key characters that have been used to separate *P. floridana* and *P. concinna* as species.

Plastral pattern was quantified by counting the number of plastral scutes that contained dark pigmentation. A number ranging from 0 to 12 was assigned to each turtle on the basis of the number of scutes containing dark pigmentation (Fig. 8). Most literature describes *P. floridana* as having an immaculate plastron, however, very few specimens in my sample completely lacked dark plastral pigmentation. I assumed individuals with low scores to be of *P. floridana* stock.

Pattern on the second costal scutes of the carapace was more difficult to score. When a large sample of specimens was examined, a gradation from the straight-line pattern of *P. floridana* to the C-shape of *P. concinna* could be observed. Five numbered categories were defined and numerical scores were assigned as follows: straight-line (1), branching (2), Y-shaped (3), X-shaped (4), and C-shaped

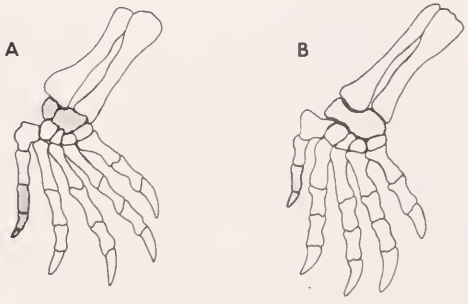

Figure 7. Bones of the hind feet; A. *Pseudemys concinna,* showing three phalanges on the fifth toe and separate astragalus and calcaneum; B. *P. floridana*, showing two phalanges on the fifth toe and a fused astragalus and calcaneum.

(5) (Fig. 9). The decision between an X-shaped and a C-shaped pattern was based upon whether the posterior branches touched the neural and marginal scutes (Fig. 9-4; X-shaped) or touched the third costal scute (Fig. 9-5; C-shaped). In some cases, especially in older specimens, this was difficult to accurately determine. If the branches were not complete a judgment as to their general direction had to be made. Right and left costal patterns were scored separately and later summed.

Four scutes make up the bridge that connects the plastron to the carapace. Specimens were scored 0 through 4 for left and right bridges separately, according to the number of scutes with dark pigmentation (Fig. 10). Scores for right and left sides were later summed. Neck striping and marginal markings were too qualitative and variable to be used in the statistical analyses.

Toe phalanx numbers on the fifth toes of the hind feet were recorded separately and later summed for use in the discriminant analysis. The astragalus fused to the calcaneum was not used since these bones were separate in all but three specimens.

A discriminant function based on four characters (plastral pattern, carapace pattern, bridge markings, and toe phalanx number) was computed using the

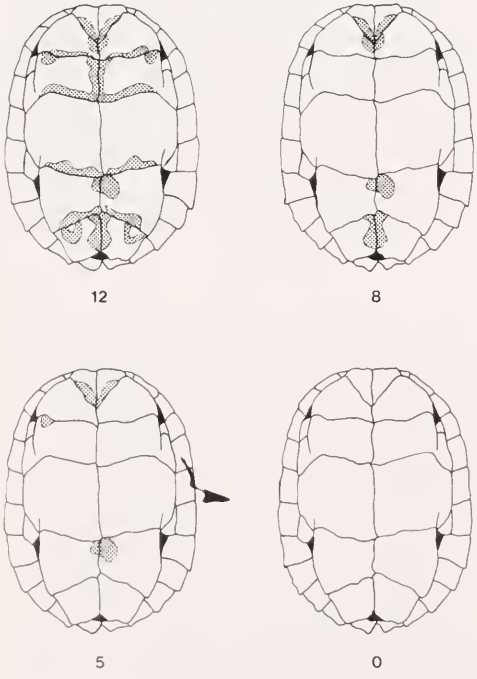

Figure 8. The scoring system for plastral patterns. Numbers indicate the number of plastral scutes containing dark pigmentation.

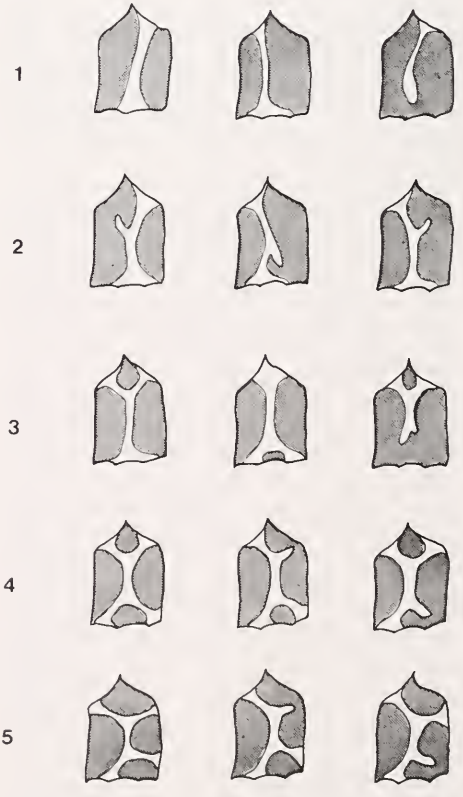

Figure 9. Scoring system used for the second costal scutes of the carapace; (1) Straight-line; (2) Branching; (3) Y-shaped; (4) X-shaped; (5) C-shaped. Three variations are shown for each category.

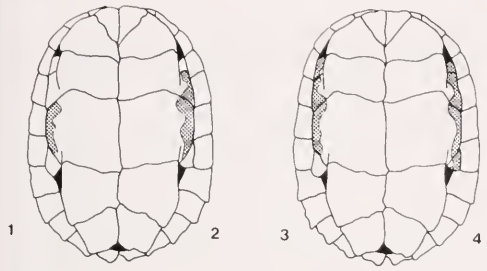

Figure 10. Scoring system used for scutes making up the bridge. Pattern categories 1 through 4 are shown through a 0 category could also be found.

BMD-04M program (Dixon, 1973). This program develops the linear function of the selected variables that gives the largest ratio of between-group variance to within-group variance. A series of discriminant coefficients is calculated to give this ratio and thus maximize discrimination between two *a priori* groups (Rao, 1952; Krishnaiah, 1966; Kendall, 1968; Gnanadesikan, 1977).

In accordance with this program, two *a priori* groups of twenty individuals each were selected from the total sample of 162 specimens; one group of specimens exhibited "pure" *P. floridana* characters, and the other "pure" *P. concinna* characters. Age and sex were not a basis for the selection of the *a priori* groups. From these *a priori* groups the set of discriminant coefficients was calculated. The sum of these coefficients times their respective character scores gave a value Z for each specimen. Using these Z-values, the program automatically classified into one group or the other all specimens not included in the *a priori* groups. By writing an addition to the program the Z-values themselves were obtained. Plotting individual Z-values on the discriminant axis showed which specimens in the unknown sample were within the range of either *a priori* group and which were intermediate (Rohwer and Kilgore, 1968; Thaeler, 1968; J.F. Jackson, 1973).

In addition to the discriminant analysis, correlation coefficients among several characters were computed using the BMD-02D program (Dixon, 1973). This program computes simple correlation coefficients. Early in this study I noticed that plastral pattern appeared to fade with age and that the number of toe phalanges on the fifth toes of the hind feet seemed to increase from 2 to 3 with age. Correlation coefficients between these characters and carapace length were computed to determine if this relationship actually existed.

RESULTS

Statistical analyses. – The results of the discriminant analysis (Fig. 11A) clearly show that, based on Z-values calculated from the four characters used, the sample does not fall into two distinct groups (species). There is also no large intermediate group that would indicate only F_1 hybridization. The sample is instead evenly distributed between, and overlaps, each *a priori* group. This indicates interbreeding of *P. concinna* and *P. floridana*, and backcrossing and interbreeding of the hybrids.

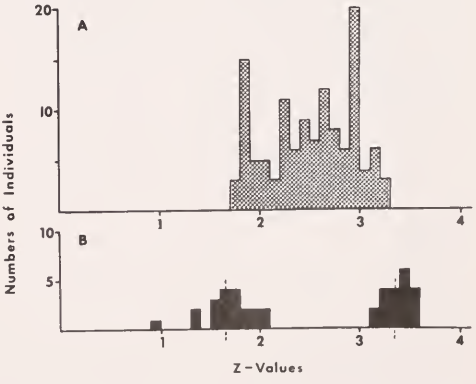

Figure 11. Histograms of specimen Z-values on discriminant axes; A. Plot of the Z-values of the unknown sample in the discriminant analysis; B. Plot of the Z-values of the *a priori* groups of *Pseudemys concinna* (mean 3.36) and *P. floridana* (mean 1.66). Dashed lines indicate the means of the *a priori* groups.

Table 1. Results of the discriminant analysis. Mean scores for each of the four characters used are shown for each a priori group along with the discriminant coefficient for each of the characters. Sample size, mean Z-value, and standard deviation for these Z-values are also given. Left and right scores have been summed for each character.

Character	P. floridana mean	P. concinna mean	Discriminant coefficient
1. Carapace pattern	3.150	9.650	0.149
2. Plastral pattern	4.850	9.750	0.037
3. Toe phalanx number	3.900	6.000	0.251
4. Bridge markings	5.350	7.750	0.007

a priori group	Sample size	Mean Z	Standard deviation Z
P. floridana	20	1.663	0.273
P. concinna	20	3.359	0.120

The mean Z-value of the *P. floridana* (1.66) and the *P. concinna* (3.36) *a priori* groups (Table 1) are well separated and the ranges of these groups have no overlap (Fig. 11B). The means for each character are also well separated (Table 1).

The range of the *P. floridana "a priori"* group was 1.14 (0.91 to 2.05) and that of the *P. concinna "a priori"* group was 0.38 (3.12 to 3.50). The range of the intermediate zone was 1.07 (2.05 to 3.12). This was slightly smaller than the range of the *P. floridana "a priori"* group. The unknown sample fills the intermediate zone, and overlaps and completely connects both *a priori* groups. Of the unknown individuals measured, 27 had Z-values that overlapped the *P. floridana "a priori"* group and 11 had Z-values that overlapped the *P. concinna "a priori"* group.

The Z-values for individuals from the five clutches hatched during this study were plotted, along with the Z-values of the females from which they were obtained, on separate discriminant axes (Fig. 12). In these figures the linear placement of genetically related individuals in the discriminant analysis is seen. In each plot the outlines of the *a priori* groups are shown. Specimens from the clutches used to make up part of the *a priori* groups are indicated by stippled squares.

Correlations computed on plastral pattern and toe phalanx number versus carapace length indicate these characters to be ontogenetically variable and not useable in taxonomy. The correlation of plastral pattern to carapace length was -0.40 which suggests a disappearance in the amount of plastral pattern as turtles grow. The correlation of toe phalanx number to carapace length was 0.45, which suggests that as turtles grow, a third phalanx on the fifth toes of the hind feet ossifies.

Qualitative characters. – Scoring of the characters jaw serration (Fig. 5), neck striping (Fig. 4), and marginal scute pattern (Fig. 6) is shown in Table 2. Jaw serration followed a gradient from strongly serrated to slighty serrated.

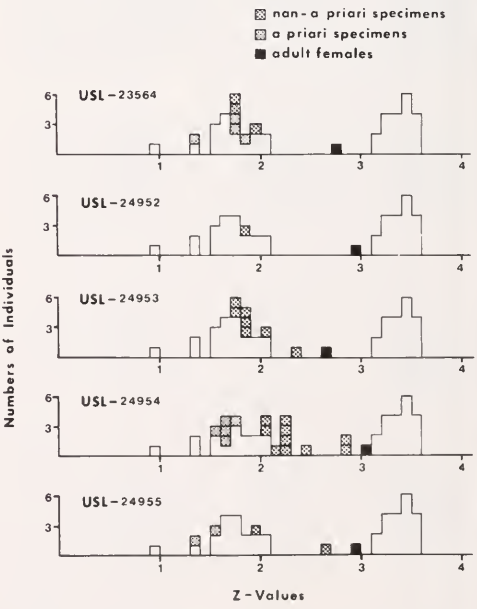

Figure 12. Plots on separate discriminant axes of the Z-values for the individual clutches from USL 23564, USL 24952, USL 24953, USL 24954, and USL 24955. Outlines of the *a priori* groups are shown. Individual specimens that were used to make up part of an *a priori* are shown by stippled squares and those not originally included in the *a priori* groups are shown by cross-hatched squares. The female from which each clutch came are shown as black squares.

For marginal scute patterns most specimens were scored as either type 2 (25.0%), with a doughnut-shaped mark, or type 3 (59.3%), with a double doughnut-shaped mark (Table 2; Fig. 6). Specimens were classified on the basis of the predominant pattern. Many specimens possessed several different types of markings.

Specimens scored for neck stripes (Fig. 4) possessed either continuous lines (31.4%) or hairpins (38.9%) on both sides of the neck. Fewer had discontinuous lines (12.5%) on both sides and the rest of the sample had mixed patterns (Table 2).

Table 2. Results of scoring the qualitative characters. Numbers of specimens for each category and percentages of the total sample are given for each character. Jaw serration and marginal scute pattern scoring systems are given in Figs. 5 and 6 respectively. Neck stripes were scored for left and right sides as: C - continuous lines, D - discontinuous lines, and H - Hairpin pattern.

Jaw serrations			
Serrated		Unserrated	
Notched (SN)	Un-notched (S)	Notched (UN)	Un-notched
54 / 33.5%	35 / 21.7%	10 / 6.2%	62 / 38.5%

Marginal Scute Pattern			
Type 1	Type 2	Type 3	Type 4
25 / 15.6%	95 / 59.3%	40 / 25.0%	0 / 0.0%

Neck Stripe Pattern					
C-C	H-H	D-D	C-H	C-D	H-D
50 / 31.4%	62 / 38.9%	20 / 12.5%	15 / 9.0%	3 / 1.8%	9 / 5.6%

Analysis of clutches. – Data from 34 hatchlings, obtained from the five gravid females, were included in the statistical analyses. Thirty-five eggs hatched, with an average incubation time of 60 days at 29° C. Many hatchlings had irregularities of shell scutes possibly caused by excessive incubation temperatures (Fowler, 1970; Vinegar, 1973, 1974). Details of each clutch are presented below:

USL 23564. – Eight individuals were hatched from the nine eggs of this female. The adult female predominantly resembled a *P. floridana*, however, the discriminant analysis placed this specimen as intermediate (Z-value of 2.70) and widely separated from its hatchlings. Seven of the hatchlings were used in discriminant analysis. One hatchling was lost. Four of the hatchlings were used to make up part of the *P. floridana* "*a priori*" group and the other three had Z-values that were clustered around the means of the *P. floridana* "*a priori*" group. Hatchlings Z-values ranged from 1.33 to 1.99 (Fig. 12). The hatchlings are catalogued as USL 24113–24119.

USL 24952. – Only one individual was hatched from 14 eggs taken from this female from Avoca Island, St. Mary Parish. The Z-value of the adult was 2.90 and close to the *P. concinna* "*a priori*" group's range though it superficially resembled a *P. floridana*. The hatchling had a Z-value of 1.87 which was within the range of the *P. floridana* "a priori" group (Fig. 12). The hatchling is catalogued as USL 24986.

USL 24953. – Seven individuals with scorable patterns hatched from 15 eggs of this female. The adult, also collected at Avoca Island, superficially resembled a *P. floridana*. All hatchlings possessed heavily pigmented plastra. The Z-values of the hatchlings ranged from 1.79 to 2.30 with all but one within the range of the *P. floridana* "*a priori*" group. The adult's Z-value was 2.60 which was well separated from all but that of one hatchling (Fig. 12). The hatchlings are catalogued as USL 24987 to 24993.

USL 24954. – The largest clutch came from this Avoca Island female. The adult possessed some *floridana*-like and some *concinna*-like characters. Fifteen hatchlings were obtained from 16 eggs. The hatchlings had a wide variety and combination of characters. The Z-values of these hatchlings ranged from 1.54 to 2.89. Five specimens from this clutch were used to make up part of the *P. floridana* "*a priori*" group. The majority of the hatchlings, however, had Z-values that placed them between the ranges of the

two *a priori* groups. The female had a Z-value (3.01) which was greater than all the hatchlings' and was well separated from all but two of the hatchlings (Fig. 12). The hatchlings are catalogued as USL 24967 – 24982.

USL 24955. – Seven eggs were taken from this female. From these, one hatchling was obtained and three embryos were removed from eggs in an advanced enough stage of development for their patterns to be scored. The adult was collected from the Atchafalaya River at Butte La Rose, St. Martin Parish. The Z-values for this clutch had the widest range of all the clutches analyzed (1.30 to 2.66). Here, as in the other clutches, the adult female had a Z-value (2.90) that was well separated from those of the hatchlings. Two of the hatchlings were used to make up part of the *P. floridana* "*a priori*" group (Fig. 12). The hatchlings are catalogued as USL 24982 – 24985.

DISCUSSION

The results from the discriminant analysis (Figs. 11 and 12; Table 1) show that the majority of the sample is intermediate on the basis of the four characters considered (plastral pattern, carapace pattern, bridge markings, and toe phalanx number). Other characters were not used in this analysis because of their wide and inconsistent range of variability. If the Z-values derived from these four characters can be assumed to be a measure of the genome then there is a complete gradation of characters from *floridana*-like to *concinna*-like individuals.

The *a priori* groups were selected by looking through the entire sample of 162 specimens and picking those whose characters nearly all were *floridana*-like or *concinna*-like. Age and sex were not used as criteria for the selection of the *a priori* groups. Calculations of Z-values show that some individuals from the unknown sample would evidently have been better choices for the *a priori* groups than some of the specimens selected. Using a sample size of 20 for each *a priori* group necessitated inclusion of some individuals whose characters were not all one extreme or the other.

If *P. floridana* and *P. concinna* were distinct species several results would be expected from the discriminant analysis. There would be a clustering of the unknown individuals around the *a priori* group means. There could be an F_1 hybrid peak somewhere between the two *a priori* groups but there should not be an even and continuous distribution of specimens from one *a priori* group to the other. The results are inconsistent with this and do not support the idea of separate species.

Figure 12 shows that all the clutches examined have a fairly wide range of characters. The clutches from USL 23564 and 24593 are grouped around the *P. floridana* "*a priori*" group. In the clutches from USL 24952, 24954, and 24955 the hatchlings' and adults' Z-values are widespread. The clutch from USL 24954 in particular has a wide range of Z-values that extend from one *a priori* group to the other. In each clutch the adult turtle's Z-value was separated from those of the majority of the hatchlings. The wide spread Z-values of these clutches and the separation of the majority of the hatchlings' Z-values from those of the adult females' are good indications of intergradation.

If *P. floridana* and *P. concinna* could be separated by a set of characters then the characters used to define each species should have a high degree of correlation. During the collection of data for this analysis I noticed that plastral pattern and toe phalanx number seemed to be related to the size of the individuals. The correla-

tion coefficients for these characters to carapace length also indicate this. Both toe phalanx number (correlation coefficient of -0.45) and plastral pattern (correlation coefficient of + 0.40) have a high correlation to shell length; this suggests that these characters are ontogenetic and of limited use as taxonomic characters. These characters were nevertheless used in the discriminant analysis since there were observable differences in them within the sample and no other characters were available.

The problem is whether these turtles should be regarded as separate species that are hybridizing or as subspecies that are intergrading. Perhaps as Carr (1952) stated, they do not fit well into our standard classification system. This problem has been compounded by several factors. Many of the original descriptions of these turtles are of limited use because the separation of species was based on locality and on sexually dimorphic characters. Their taxonomy at the present is based only on qualitative characters of color and pattern. Most studies of these species have dealt with only small segments of the ranges of these turtles.

In the original descriptions Le Conte (1830) described *Testudo floridana* and *T. concinna* and differentiated between them primarily on the basis of color and pattern. He mentioned differences in the shape of the carapacial scutes which can probably be attributed to the sex and size of the specimens used in his descriptions. The *T. floridana* he described was 15 inches (37.5 cm) long and the *T. concinna* was only 8 inches (20.3 cm) long. Carapacial scutes change shape as the turtles grow. Other than these scute differences LeConte differentiated between the two only by the pattern of yellow lines on the carapace.

Holbrook (1836 to 1838) described *Fmys hieroglyphica* and *E. mobilensis,* and also listed *E. concinna* and *E. floridana.* His descriptions, like those of LeConte, were based primarily on color and pattern. He also relied heavily on the location from which the specimens were taken for identification. His descriptions of all four turtles were similar; major differences were related mostly to sexually dimorphic and ontogenetic characters of the specimens.

All populations studied by Carr (1935, 1937, 1938, 1952) were considered by him to be subspecies of *P. floridana* since wherever any came into contact they interbred, and no characters could be used to reliably separate them. There appeared to be one exception to his uniform intergradation. Two of the subspecies, *P.f. peninsularis* and *P.f. suwanniensis*, seemed to maintain nearly complete reproductive isolation. The other subspecies *of P. floridana* were geographic subspecies; *P.f. peninsularis* and *P.f. suwanniensis* appeared to be ecological subspecies, separated by the preference of different habitats.

Crenshaw's (1955) division of the *P. floridana* complex into two species is based on the reproductive isolation maintained between *P.c. suwanniensis* and *P.f. peninsularis.* This division is founded upon an exception and not what normally occurs throughout the species ranges.

Crenshaw mentioned the occasional hybridization between *P.f. peninsularis* and *P.c. suwanniensis* but stated that it was believed to be secondary intergradation and rare. He also stated, "Evidence of introgressive hybridization and frequency of strongly intermediate specimens of the *floridana* and *concinna* groups increases progressively as one moves away from peninsular Florida into other areas of the U.S., however, relatively typical examples of each group occur throughout the area of geographic overlap of the two groups."

Crenshaw concluded that, "Relationships between members of the *P. floridana* complex will be more nearly reflected by subdividing the complex into two species." This was true for *P.f. peninsularis* and *P.c. suwanniensis* in Florida but not for the other subspecies throughout their respective ranges. Along with work of other researchers, my data indicate a large amount of intergradation in most areas of the ranges of these turtles (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Crenshaw's work showed that *P. concinna* and *P. floridana* were closely related and intergrading but it did not conclusively show that they should be regarded as separate species.

Pritchard (1967) is the only recent author who has followed Carr's scheme. He mentioned difficulty in identification of subspecies because of extensive hybridization and the fact that some of the subspecies are not easily distinguishable from one another. He felt that separation into *P. floridana* and *P. concinna* was incorrect since the two intergrade completely.

Mayr (1963) defined species as, "groups of interbreeding natural populations that are reproductively isolated from other such groups." This definition is based primarily on reproductive isolation. Mayr listed various situations in which it would be difficult to apply this definition. Four of these situations are (1) morphological differentiation without reproductive isolation, (2) reproductive isolation dependent upon habitat isolation, (3) incompleteness of isolating mechanisms, and (4) the achievement of different levels of speciation within different populations. These four situations have possible application to the *P. floridana–concinna* complex.

Some authors (Ernst and Barbour, 1972; Conant, 1975) indicate that *P. floridana* and *P. concinna* occupy or once occupied different habitats. Possibly they have differentiated morphologically because of the different selective pressures in these habitats but have not developed any form of reproductive isolation before re-establishing contact with each other. Without reproductive isolation turtles differing morphologically may have interbred, producing offspring with a variety of characteristics. Many of these characteristics may not be useable as taxonomic characters to separate the two as species.

My data indicate that in the lower Red, Atchafalaya, and Mississippi river basins there is a large amount of interbreeding. Other workers (Brown, 1950; Smith, 1961; Anderson, 1965; Webb, 1970; Barbour, 1971; Mount, 1976) have also indicated the occurrence of interbreeding in other areas. The isolating mechanisms, if they exist, do not appear to be well established. Even in Florida the reproductive isolation of *P.f. peninsularis* and *P.c. suwanniensis* is not complete though interbreeding is rare (Crenshaw, 1952).

In nearly all areas of contact between *P. floridana* and *P. concinna* interbreeding has been observed, but in a few areas where there are distinct and separate habitats, interbreeding is rare (Smith, 1961; Pritchard, 1967; Barbour, 1971; Keiser, 1976; Mount, 1976). Contact between populations seems to be the most important limiting factor of reproductive isolation.

The lower Mississippi River drainage in Louisiana is an area where frequent contact between these turtles could be expected. Here the aquatic habitats are not as well defined as in many other areas of these species' ranges. Periodic flooding tends to mix geographically separated populations more often. Because of the increased contact *P. floridana* and *P. concinna* probably interbreed more in

this area than in many others and as a result have greater genetic similarity here.

Though Mayr (1963) stresses reproductive isolation as the prime factor separating species, it is not synonymous with noninterbreeding. Two species can interbreed and be reproductively isolated (Bigelow, 1965). Interbreeding can occur with little effect if the progeny are incompatible with the parent species. What is important is the flow or introgression of genes from one species to the other. My data indicate that introgression has taken place and implies a high degree of compatibility between *P. floridana* and *P. concinna*.

Grant (1963) described various population systems and used the term "semispecies" to refer to a population system having properties of both races and species. Following his classification system *P. floridana* and *P. concinna* would be classified as "sympatric semispecies" which are, "population systems intergrading discontinuously or partially and judged to be interbreeding on a restricted scale, they are sympatric and only partially isolated reproductively." Grant's classification offers a basis for argument that *P. floridana* and *P. concinna* are "ecological races" which are, "population systems intergrading continuously in morphological or physiological characters and judged to be interbreeding freely." Grant's classification would not classify *P. floridana* and *P. concinna* as separate species.

Both Grant's and Mayr's systems for classifying populations and species are useful as possible explanations of the relationship between *P. floridana* and *P. concinna*. The exact nature of the relationship cannot be determined except by long term breeding experiments. There is definite intergradation within the lower Red, Atchafalaya, and Mississippi river basins. The isolating mechanisms between *P. floridana* and *P. concinna* are weak if they exist. There is a complete gradation of characters and the characters presently used to separate these turtles into two species are probably useless. Apparently either a large hybrid swarm (a population that forms a continuous bridge between two parental species due to a breakdown in the isolating mechanisms) is present or two or more subspecies are merging within this area.

CONCLUSIONS

1. The discriminant analysis based on four characters (plastral pattern, carapace pattern, toe phalanx number, and bridge markings) has shown the following:
   - A. The specimens of the sample were not distinguishable as *Pseudemys floridana* and *P. concinna* but the majority were instead intermediate.
   - B. These four characters are of little or no taxonomic value in separating these turtles since there was found to be a complete and even gradation from *floridana*-like to *concinna*-like specimens.
   - C. The wide range of Z-values found within individual clutches indicates interbreeding of specimens with widely varying characteristics.
2. Plastral pattern was found to fade with age and was highly variable within individual clutches. This character is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.
3. Toe phalanx number on the fifth toes of the hind feet appears to increase from two to three with age and is of little or no taxonomic value for the separation of *P. concinna* and *P. floridana*.
4. Because the majority of the sample of Louisiana specimens possesses inter-

mediate characters, and appears to be part of one continuously interbreeding population, I propose that the scheme of Carr (1952) be followed. Accordingly *Pseudemys concinna* and *Pseudemys floridana* are synonymized under the senior synonym, *Pseudemys floridana* until there may be quantitative characters to definitively distinguish the forms *floridana* and *concinna* as separate species.

ACKNOWLEDGMENTS

I express my greatest appreciation to my major professors, Drs. Edmund D. Keiser and Darryl L. Felder. I gratefully acknowledge Dr. Felder for his serving as major professor, in the absence of Dr. Keiser, and for his editing and constructive criticism during the preparation of this manuscript. Many of the data presented in this manuscript were collected while I was a research assistant to Dr. Keiser, and some portions of the raw data were previously reported in his *Herpetofaunal Survey of the Atchafalaya River Basin* (1976); I thank Dr. Keiser for permission to use these data. I would also like to thank the members of my committee Drs. Matt E. Dakin, Walter O. Durio, and H.D. Hoese. I thank Dr. James Jackson for his help with the statistical procedures and Drs. Douglas Rossman (Louisiana State University) and Harold Dundee (Tulane University) for their advice and the loan of specimens. Dr. Thomas Rizutto and graduate assistant Pat Walsh aided with the statistical procedures. Garland Barras X-rayed adult turtles and Michel Kirton helped with the graphics and field work. The following people also aided in the field: James Rives, Steven Barnes, Eric Couvillon, John Carter, Alan Pounds, Floyd Mason, George Picou, and Dr. Keiser.

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APPENDIX I

USL and Tulane University specimens used in the statistical analyses of this tudy. Specimens are listed by locality and parish alphabetically.

USL specimens. – Big Alabama Bayou (Point Coupee): 24034, 24094-24100, 25017. Little Alabama Bayou (Point Coupee): 23646, 23647, 24101-24106, 25018-25047, 25054-25057. East Outer Levee 5 mi. N. I-10 (Point Coupee): 25011-25013. False River (Point Coupee): 20195. Bayou Courtableau (St. Landry): 23566-23577, 24024-24026, 24028-24029, 24033, 25048-25052. Bayou Courtableau at West Outer Levee (St. Landry): 25014-25016. Indian Bayou Hunting Club (St. Landry): 22222. Krotz Springs (St. Landry): 23261. Atchafalaya River (St. Martin): 24955, 24982-24985. Butte La Rose (St. Martin): 25053. Butte La Rose Bayou (St. Martin): 14170, 14383, 14484, 15113, 23565, 25062. Whiskey Bay (St. Martin): 23564, 24113-24119, 25058. Avoca Island (St. Mary): 24952-24954, 24967-24981, 24986-24993.

Tulane specimens. – Caddo Lake (Caddo): 458, 632, 633, 647, 657, 658, 734, 735. Tensas River, Clayton (Concordia): 16042.0-16042.6. Lake Providence (East Carroll): 826. Waggamon Pond (Jefferson): 5772-5774, 5874, 5879, 5975, 5876. Lake Arthur (Jefferson Davis): 1104. Bayou Gauche (St. Charles): 13756.2. Lake Pontchartrain (St. Charles): 13571, 16038. Chauvin (Terrebone): 13618.

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ERRATA

Tulane Studies in Zoology and Botany Volume 22, number 2

In the article by Porras, McCranie and Wilson the following errors should be noted. The authors did not see final proofs and are not responsible for the errata.

P. 87, col. 1, line 42 — *Bothriopsis* should read *Brothriopsis*

P. 87, col. 1, line 44 — *Brothriopsis* should read *Bothriopsis*

P. 87, col. 2, line 11 — 1935: 22 should read 1935: 222

P. 87, col. 2, line 37 — 81.4% should read 81.6%

P. 87, col. 2, line 39 — 67.7% should read 69.7%

P. 87, col. 2, line 40 — x should read $\bar{x}$

P. 88, col. 2, line 12 — Xuantunich should read Xunántunich

P. 102, col. 2, lines 6 and 7 — Vanzolini and Williams, 70 should read Vanzolini and Williams, 1970

P. 102, col. 2, line 7 — Duellmn should read Duellman

P. 102, col. 2, line 8 — Duellmn should read Duellman

P. 103, col. 1, line 29 — UMNZ should read UMMZ

P. 103, col. 1, line 46 — USNM 22422 should read 22442

P. 104, col. 1, line 19 — Xuanantunich should read Xunántunich

P. 104, col. 1, line 22 — Posada-Arango, 1889 should read Posada-Arango, 1889a, 1889b

P. 105, col. 1, line 7 — Ophedia should read Ophidia

P. 105, col. 1, line 20 — 2Trimeresurus should read *Trimeresurus*

P. 105, col. 2, line 45 — *ophryomega* should read *ophryomegas*

P. 106, col. 1, line 41 — Buck should read Buckley

P. 107, col. 1, lines 1 - 5 — Information is out of place; it should come after Schmidt, 1933 as a continuation of the first two lines of that citation.

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Volume 22, Number 2 $3.50 May 3, 1981

LIFE HISTORY PATTERN OF *NOTROPIS SABINAE* (PISCES: CYPRINIDAE) IN THE LOWER SABINE RIVER DRAINAGE OF LOUISIANA AND TEXAS

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ABSTRACT

The life history of *Notropis sabinae* in two tributary streams of the lower Sabine River drainage system (Bayou Anacoco, Beauregard-Vernon Parish line, Louisiana; Big Cow Creek, Newton County, Texas) was studied from 1972 to 1977. The life history pattern observed for the two streams was similar. In Bayou Anacoco, the reproductive season extended from early April through late September; it was similar in Big Cow Creek except that reproduction ended earlier in September 1973. Counts of unovulated mature ova in females ranged from 113 to 423 for females 35-48 mm SL and were significantly correlated with female size. There was a low but significant correlation between the ovary weight-somatic weight ratio and body size among Bayou Anacoco females, but not among Big Cow Creek females. A low but significant correlation was found between mean mature ovum size and body size among females from both localities. The size of unovulated mature ova ranged from 0.55 to 0.88 mm diameter. There were no significant differences in slope or elevation of regression lines fitted to either fecundity or ova size data for each of the two localities. Sex ratios did not differ significantly from 1:1. Females matured at a slightly larger size than males; all females were mature by 32 mm in Bayou Anacoco and 33 mm in Big Cow Creek. Mean sizes of adult males and females did not differ significantly. Maximum age for most individuals of *Notropis sabinae* was about 1½ to 2 years. Maximum size was 49 and 47 mm SL for Big Cow Creek and Bayou Anacoco, respectively.

INTRODUCTION

Information on the life history of the Sabine shiner, *Notropis sabinae* Jordan and Gilbert, is almost completely lacking. Except for data on habitat and distribution, only ancillary comments are available (cf. Moore, 1944; Douglas, 1974; Pflieger, 1975). The reproduction, age and growth of *N. sabinae* are considered herein.

This species is a member of the *Notropis longirostris* species group (subgenus *Alburnops*; Swift, 1970), which also includes *N. longirostris* and an undescribed species in the Mobile Bay drainage system. The species in this group are common inhabitants of clear, small to moderate sized sand-bottomed streams of Gulf coastal plain drainages. *N. sabinae* occurs in such streams of the Calcasieu, Sabine and Neches river drainages of southwestern Louisiana and southeastern Texas; it is also present in the White and St. Francis river systems of Arkansas and Missouri (Moore, 1968; Pflieger, 1971, 1975; Buchanan, 1973; Douglas,1974). Douglas, (1974) also reported an isolated population in the Little River system of east-central Louisiana.

MATERIALS AND METHODS

Monthly collections were obtained from Bayou Anacoco below State Hwy. 111, Beauregard-Vernon Parish line, Louisiana (T. 2 S., R. 11 W., SE ¼ sec. 20). The stream receives Kraft papermill effluent above this locality; therefore,

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another stream was sampled to provide a "check" on data from Bayou Anacoco. The second locality consisted of access points along Big Cow Creek for ca. 0.8 - 1.2 km from Farm Road 1416, Newton County, Texas. The sampling locality in Big Cow Creek was about 39 km SSW of that in Bayou Anacoco. Collections were made from December 1972 (March 1973 at Big Cow Creek) through November 1973 with 3-m long, 4.8-mm and 3.2-mm Ace mesh seines. Supplementary collections were made during the springs of 1974, 1976 and 1977. Fishes were initially preserved in 10% formalin and stored in 43% isopropyl alcohol. Specimens were deposited in the Tulane University Museum of Natural History.

Stream flow records were obtained from local offices of the United States Geological Survey (Baton Rouge, LA; Austin, TX). The gauging station on Bayou Anacoco was located at my sampling locality; however, the gauging station on Big Cow Creek was located at State Hwy. 87 ca. 35 km upstream from my sampling point. Water quality data for Bayou Anacoco were also secured; no such data were available for Big Cow Creek. Climatological and daylength data for nearby recording stations were obtained from the National Climatic Center, Asheville, North Carolina, and the Naval Obsrvatory, Washington, D.C., respectively.

Periodic changes in the reproductive condition of females were determined by measurements of ova, determination of ovarian weights, and gross examinations of ovaries of females in the monthly samples. Both ovaries were removed from each of 10 adult females (when available) chosen at random from each collection examined. The diameter of one of the larger eggs from each female was measured. Preserved ova were not spherical; thus diameters were estimated by averaging measurements of the largest and smallest dimensions. Measurements were made to the nearest 0.05 mm using an ocular micrometer in a dissecting microscope. Ovaries and specimens were dried to a constant weight at 100-105°C and weighed to the nearest 0.001 g; ovarian weight was calculated as a percentage of total body weight. Contents of the digestive tract were removed before drying to eliminate a possible source of variation in data. Gross assessments of reproductive condition were based on the classification of females into one of the following stages of ovarian condition: (1) Immature (IM) – ovaries very small, thin, transparent to slightly translucent. Larger, developing ova, if present, yolkless with nucleus visible. (2) Early maturing (EM) – ovaries small to moderate size, translucent to white in color. Larger eggs relatively small with nucleus obscured by yolk deposition, often numerous, and becoming white in color. (3) Late maturing (LM) – ovaries greatly enlarged, filling a large portion of the body cavity, white to cream color. Larger maturing ova often as large as mature ova but not easily differentiated from smaller maturing ova, usually cream colored. (4) Mature (MA) – ovaries greatly enlarged, filling a major portion of the body cavity and usually distending the abdomen, cream to yellow. Mature ova present, cream to yellow in color, easily differentiated from maturing ova on the basis of size and color, and relatively numerous. (5) Partially spent (PS) – ovary noticeably smaller than mature ovary, relatively small number of mature ova present, often translucent areas and/or areas of small maturing ova easily distinguishable among larger mature ova. All individuals capable of producing gametes were considered sexually mature adults. More specifically, females were considered sexually mature if they had at least three enlarged eggs with the nuclei obscured by yolk deposition in one ovary (usually left) examined from each specimen. Individuals classified as MA or PS were considered reproductive. Breeding coloration, tuberculation and enlargement of urogenital papillae were also noted.

To illustrate the ova development pattern in *N. sabinae*, an ova diameter histogram was prepared using a mature female. All eggs in one ovary with the nuclei obscured by yolk deposition were measured. The number in each 0.05 mm size group was plotted as a percentage of the total number measured.

Analysis of reproductive condition in males was based on tuberculation and gross examination of the testes. Maturity was assessed primarily on the basis of increased size and development of opaque white testes in comparison to the smaller transparent/translucent testes of immature males.

Fecundity was determined by direct counts of mature ova in ovaries of reproductively mature females. Generally the specimens examined were only those with abdomens distended as a result of the ovaries filling the body cavity. Mature ova were easily separated from maturing ova on the basis of size and color. For each of the females examined for the analysis of fecundity, ten mature ova were chosen at random and their diameters measured to determine mean mature ovum diameter. Ovaries and specimens were dried and weights determined for calculation of ovarian weight-somatic weight ratios. Covariance analyses of these data were conducted following Snedecor and Cochran (1967).

Analyses of size at sexual maturity, sex ratio and mean size of sexually mature males and females were based on a number of collections. Chi-square tests (X^2) were used in replicated tests for goodness of fit to determine if there were significant deviations from a 1:1 sex ratio ; average sizes of adult males and females were compared using the unweighted means analysis in a two-way analysis of variance (Steel and Torrie, 1960; Snedecor and Cochran, 1967; Sokal and Rohlf, 1969).

Estimates of age were made on the basis of length frequency and scale analyses. All individuals in each collection analyzed were measured to the nearest 0.1 mm standard length (SL) and length frequency histograms prepared by plotting the percentage frequency for each 1-mm size group. For scale analyses, about 10-20 scales were removed from the area above the lateral line and anterior to the dorsal fin insertion of each specimen examined. Scales were cleaned by rubbing between two fingers moistened with water, mounted between two glass slides, and observed by microprojection at 50X. Annuli were identified by various combinations of the following: cutting over of circuli in dorsal and ventral fields, discontinuity of circuli or ridge-spacing in the posterior field, thickening of circuli and bending of radii.

STUDY AREAS

The stream at the Bayou Anacoco locality normally ranged from ca. 15-38 m in width. The area consisted of flowing runs and/or riffles 0.6m or greater in depth; they stretched between sandbars which constituted about 30-40% of the total shoreline, the remainder being heavily wooded. The bottom was primarily comprised of white sand with some gravel intermixed in patches; at times it became covered with a light layer of silt and/or detritus. With a gradient of 0.5 m/km in the immediate area, stream flow was usually moderate or slightly greater. The average discharge for the period of August 1969 – September 1973 was 0.013 $m^3/s/km$ with an average annual runoff of 401 mm.

Bayou Anacoco was typically dark brown in color, presumably resulting largely from the papermill effluents. For example, monthly measurements of color for 1972-76 (excepting October 1972 – May 1973, August – October and December 1976) averaged 100 platinum cobalt color units, range from 20-400 units. Other physicochemical characteristics recorded over the same time period were as follows (mean followed by (range): dissolved oxygen, 7.4

ppm (5.3-10.0); pH, 6.9 (6.2-7.8); alkalinity 29 mg/1 (8-87); and specific conductance, 206 micromhos/cm(41-629).

The stream section sampled in Big Cow Creek was narrower and sandbars were much less extensive and more intermittent. This area probably represents the upper reaches of the tributary in which *N. sabinae* occurs in relatively large numbers. The stream usually ranged from ca. 15-24 m in width with a section of this area divided into two channels normally ca. 9-12 m wide. The stream bed was similar to that in Bayou Anacoco. Stream flow was usually moderate; the gradient in the immediate area was 0.5 m/km. Average discharge for the 24 year period April 1952 – September 1976 was 0.009 $m^3/s/km^2$, the average annual runoff 296 mm.

Mean annual temperature in the area (Kirbyville Forest Service, TX. and Elizabeth, LA, stations) was 19°C. Mean temperature in January was 10°C and in July 28°C. Average annual rainfall was 150 cm.

RESULTS

Species Associates — A total of 45 species was taken from Bayou Anacoco; 38 were taken from Big Cow Creek. *Notropis sabinae* was the second most abundant species in each area, constituting 31% and 23% of all specimens collected from Bayou Anacoco and Big Cow Creek, respectively. *Notropis venustus* was the most abundant species; it composed 37% and 33% of all samples from the two respective stations. An association similar to that of *Notropis longirostris, Notropis venustus* and *Ammocrypta beani* (Heins and Clemmer, 1975) existed between *N. sabinae, N. venustus* and *Ammocrypta vivax* in these streams. *Notropis sabinae* and *N. venustus* were always taken together; and although *A. vivax* was not as abundant (3% of all samples from each locality), it was taken frequently (94 and 92 percent frequency of occurrence, n=16, 13, respectively). Both *N. sabinae* and *A. vivax* occupied the same open sand bottoms along sandbars, although *A .vivax* tended to be more abundant in areas of mixed sand and gravel. Other species collected were not closely associated nor commonly taken with *N. sabinae.* A complete list of species taken at each locality (including relative abundance and frequency of occurrence) is available in Heins (1979).

Reproduction – Secondary sexual characteristics: The extent of tubercle development may vary considerably in reproductively mature *N. sabinae* males. Weakly tuberculate males had small to moderately large, fine tubercles scattered over the sides of the snout (separated by wide hiatus at the tip of the snout) and lateral areas of the head posteriorally from the anterior edge of the lacrimal to the anterior suborbital area; small widely scattered tubercles often extended to the angle of the preopercle. Tubercles on the side of the head were separated from those on the snout by a sometimes poorly defined hiatus along the anterior edge of the lacrimal. Highly tuberculate males (Fig. 1) had concentrations of large, slightly retrorse to erect tubercles on each side of the snout which were separated by a hiatus of variable size at the tip of the snout. Tubercles on the lateral areas of the head extended from the anterior edge of the lacrimal (large to moderately large, erect to slightly retrorse) posteroventrally to the angle of the preopercle, generally becoming smaller and erect and at times sparsely scattered. Tubercles in the anterior suborbital area also tended to be smaller. Small to moderate size tubercles occurred between the orbit and nares and were separated from the anterior suborbital tubercles; they extended to the antero-dorsal aspect of the orbital margin and were occasionally absent. Small to moderate size tubercles were variably developed in two small groups medial and slightly anterior to the nostrils; at times the groups were poorly

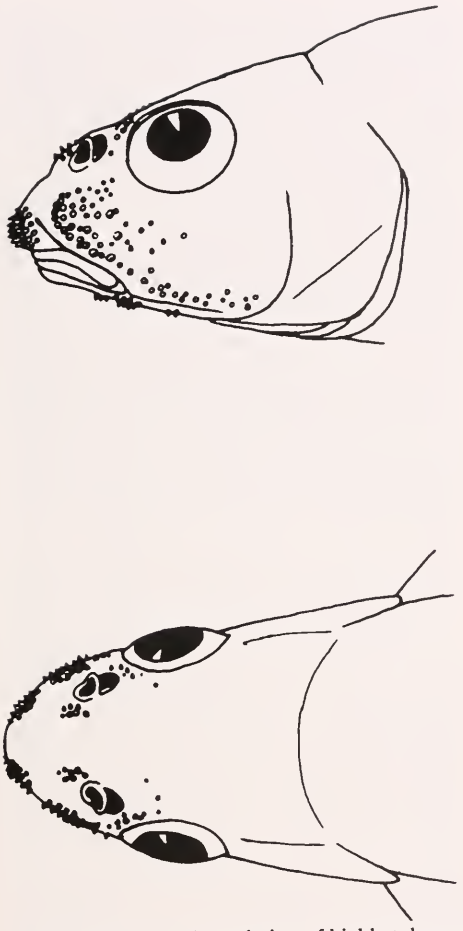

Figure 1. Head tuberculation of highly tuberculate *Notropis sabinae* males. The drawing is a composite of a number of specimens.

separated. Occasionally small scattered tubercles occurred between the orbits. Small to moderately large tubercles were variably developed on the posterior half of the mandibles of most males, forming one or two poorly defined rows in highly tuberculate males; occasionally a few also developed on the lower arm of the interopercle. Minute tubercles formed a shagreen on the pectoral rays of most males, the greatest development was generally on rays 2-6, less so on 7; they usually originated about one-fourth of the distance from the proximal end of the rays and extended to just past the first, major branching. Tubercles were occasionally scattered on other rays and the dital ends of hevily tuberculated rays. Tubercles also occured on dorsal, pelvic and anal fins but were poorly developed. No tubercles were noted on body scales.

Tuberculation in reproductively mature females was generally very weak. Some females developed small to fine tubercles that were scattered over the sides of the snout and head posteriorly to the suborbital areas. Tubercles occasionally extended to the angle of the preopercle or were on the mandible. Minute tubercles occasionally were also scattered along rays of the pectoral fins.

Reproductive coloration is poorly developed in both sexes, particularly in females. A faint lemon yellow color often develops in the dorsal and caudal rays of males, being strongest antero-basally. White pigmentation is also variably present in these and other fins, particularly the pectoral and anal. Breeding females have enlarged urogenital papillae which are absent in males.

Reproductive periodicity in females: Periodic changes in ova diameters and ovarian weights (Fig. 2) and gross ovarian examinations demonstrated a reproductive season extending from early April through late September in Bayou Anacoco. Diameters of ova and ovary weights were small from December 1972 through mid-March 1973 ($\bar{X}$ = 0.17—0.27 mm, 0.9-1.2% body weight). These measurements were slightly greater in late March 1976, but all females examined (n = 21) were still maturing as they were in 1973 (n = 18). No sample was available from April 1973 due to flooding during the scheduled sampling period. Females were in reproductive condition in early April of 1974 (93% MA&PS, n = 30) and 1976 (32% MA&PS, n = 37); diameters of ova averaged 0.71 and 0.53 mm and ovarian weights 6.1% and 3.7% of body weight, respectively. These data also indicate that reproductive activities began somewhat later in 1976. Females were in re-

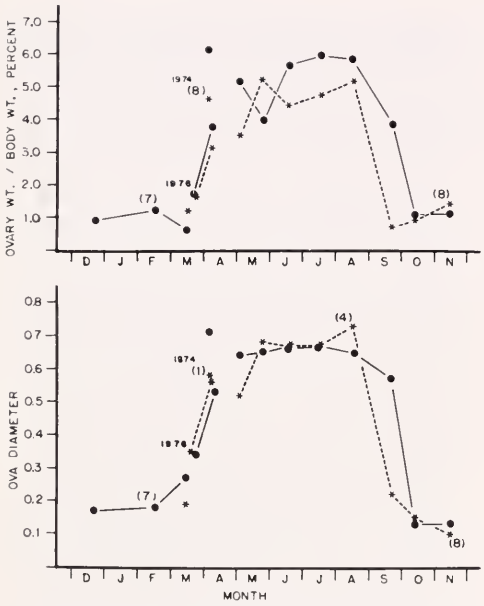

Figure 2. Mean diameter of largest ova (lower graph) and mean percentage ovary weight (upper graph) for *Notropis sabinae* from Big Cow Creek, Texas (dashed lines), and Bayou Anacoco, Louisiana (solid lines), 1972-73 (no April sample), April 1974, and March-April 1976. Lines connect only data points for sequential samples within the same year. Numbers in parentheses indicate the number of observations on the mean when less than ten. Statistics of variability are available in Heins (1979).

productive condition in early May 1973, (63% MA&PS, n = 30). Ova diameters and ovarian weights remained large from May through late September 1973 ($\bar{X}$ = 0.57 - 0.67 mm, 3.8% - 5.9% body weight). In September, 77% (n = 26) of the females were reproductive. Ova diameters and ovarian weights decreased to an average of 0.13 mm and 1.0% of body weight by mid-October, and almost all females were considered non-reproductive (98% IM&EM, n = 55). The reproductive periodicity of females in Big Cow Creek was similar to that in Bayou Anacoco (Fig. 2), but reproduction ended somewhat earlier in 1973. Diameters of ova and ovarian weights decreased to 0.22 mm and 0.7% of body weight by late September, and only 2 of 32 females (6%) were considered reproductive. The periodicity and variability in temperature, photoperiod and stream flow accompanying these cycles are shown in Figure 3.

After attaining reproductive condition, individual females remained reproductive throughout the spawning season. Maturing ova were present in reproducing females throughout the season. The ova development pattern of this species exhibits two complements of yolk-bearing ova, a stock of smaller maturing ova and a differentiated group of larger mature ova (Fig. 4). Such a bimodal distributions is indicative of a variable series of spawnings with complements of ova released periodically over an extended reproductive season (Hickling and Rutenberg, 1936; Prabhu, 1956; Qasim and Qayyum, 1961; MacGregor, 1970).

Reproductive periodicity in males: The cycles of testis and tubercle development were similar for both areas. Males taken in December and February had no tubercles although there were scars on a few; testes were small and cloudy to white in color. In March samples testicular activity was indicated by enlargement of the testes; tubercles also developed in March. Testes and tubercles were generally well developed from April into September; however, there was a decline of testis and particularly tubercle development in Big Cow Creek males in September, coincident with the decline of reproductive activity in females. Testes were small in October and November. Very small degenerating tubercles were still present in October but were generally absent in November, excepting tubercle scars in some males.

Reproductive effort and ovum size: There was a highly significant correlation between number of mature ova and standard length among females from both localities (Table 1). Regression lines expressing the relationship between counts of mature ova and body size did not differ in slope ($F = 0.14$; $df = 1, 60$; $p > .05$) or elevation ($F = 2.20$; $df =$

1, 61; $p > .05$) when tested by analyses of covariance; therefore, the data from both localities were combined. Counts of mature ova ranged from 113 to 423 for females 35.4 - 47.8 mm SL. The intercept, regression coefficient and correlation coefficient for the linear relationship between fecundity and standard length among females in the combined sample (Fig. 5, $r^2 = 0.57$) are also given in Table 1. Log-log and semi-logarithmic transformations yielded similar r^2 values, indicating that any of the three models adequately defined the relationship. However, logarithmic transformation of both variables stabilizes the variance along the regression line (Bagenal, 1967) and is important for use in prediction; the resulting equation is ($r^2 = 0.53$; F = fecundity, SL = standard length):

$$\log_{10}F = -2.8297 + 3.1953(\log_{10}SL).$$

There was a low but significant correlation between ovarian weight-somatic weight ratio and body size among females from Bayou Anacoco, but there was no significant correlation among females from Big Cow Creek (Table 1, Fig. 6). This notwithstanding, there was a low but highly significant correlation between ovarian weight-somatic weight ratio and body size among females in the combined samples. In general, these ratios ranged from 4.8 -15.2%.

There was a low but significant correlation between mean mature ovum size

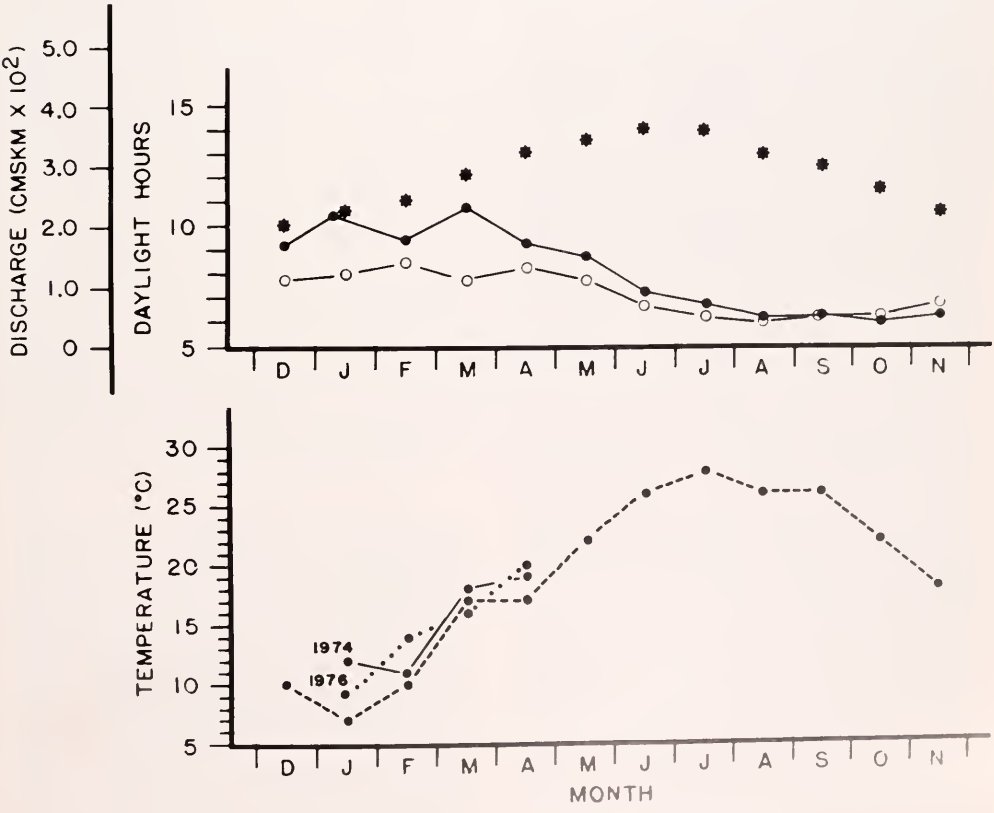

Figure 3. Environmental variability and periodicity for Big Cow Creek, Texas, and Bayou Anacoco, Louisiana. Upper graph: mean monthly number of daylight hours (bold asterisks, Lake Charles, LA) and mean monthly discharge as cubic meters per second per square kilometer for Big Cow Creek (1952-76, open circles, solid line) and Bayou Anacoco (1969-73, solid circles, solid line). Lower graph: mean monthly air temperature for 1973 (dashed line, DeRidder, LA), early 1974 (solid line), early 1976 (dotted line).

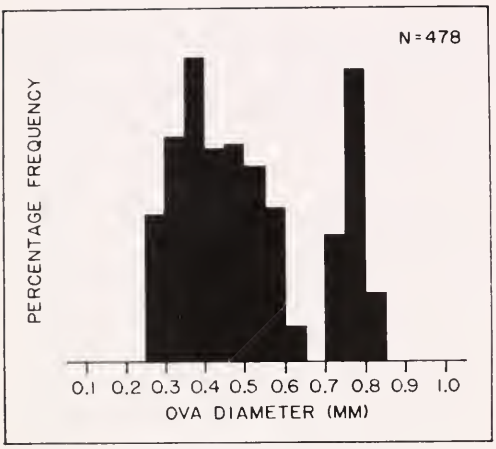

Figure 4. Size frequency distribution for vitellogenic ova in a reproductive *Notropis sabinae* female, indicating the typical pattern of ova maturation and recruitment.

and body size among females from both localities (Table 1, Fig. 7), indicating a tendency for larger females to produce larger ova. Data are missing for one specimen fromBayou Anacoco; the ovary was not well preserved and many eggs broke when teased from the follicles. Analysis of covariance showed that regression lines fitted to the data for each locality did not differ in slope ($F = 0.53$; $df = 1, 59$; $p > .05$) or elevation ($F = 2.03$; $df = 1, 60$; $p > .05$); therefore, data for both localities can be combined. The mean sizes of the mature ova measured ranged from 0.63 to 0.81 mm diameter and averaged 0.72 mm ($S = 0.0452$). Addition of mean mature ovum diameter to the linear equation for fecundity did not significantly increase the r^2 value ($F = 2.260$; $df = 1, 60$; $p > 0.05$).

Sex ratio, size at maturity and mean size of adult males and females: Chi-square tests indicated that there were no significant differences from a 1:1 sex ratio at either locality. The heterogeneity χ^2 was not significant ($p > .05$) for either Big Cow Creek (0.7485, $df = 4$) or Bayou Anacoco (5.3745, $df = 4$); similar results were obtained for the pooled χ^2 at the two respective stations (2.9823, $df = 1$; 1.6864, $df = 1$).

The number of specimens originally examined from Big Cow Creek to determine size at sexual maturity was insufficient; therefore, supplemental specimens taken in August 1973 and a portion of those taken in May 1977 were also examined. The supplemental specimens appeared to differ somewhat from those initially examined (May–July 1973) in that individuals seemed to mature at a

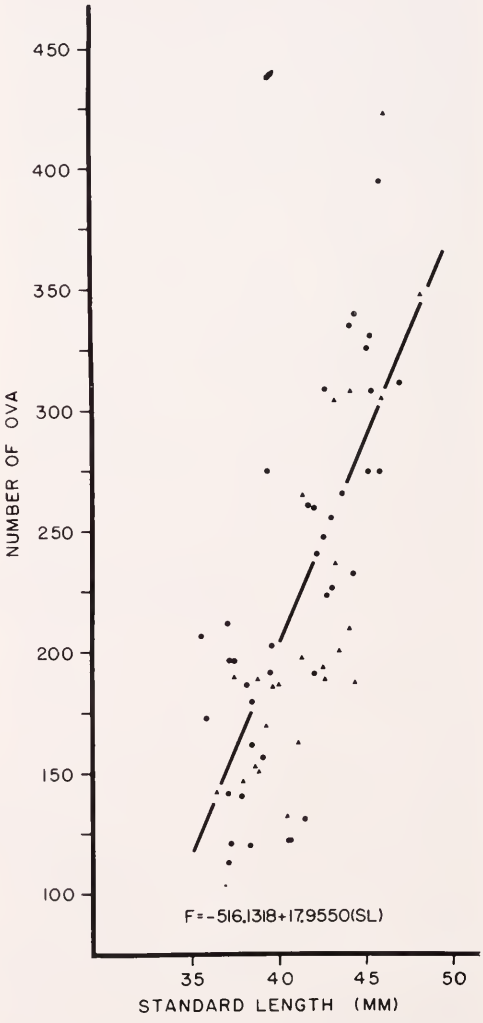

Figure 5. Relationship between number of mature ova and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

Table 1. Summary of linear regression analyses of ova number-body size, ovary weight-somatic weight ratio--body size, and ova diameter-body size relationships for samples of *Notropis sabinae* from Big Cow Creek, Texas, and Bayou Anacoco, Louisiana, 1973-1974 and 1976-1977; ns = non-significant difference, * = significant difference at .05 level, ** = significant difference at .01 level.

Ova number-body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24	−581.3956	19.2567	.772**
Anacoco	40	−497.7474	17.6721	.758**
COMBINED	64	−516.1318	17.9550	.753**

Ovary weight-somatic weight ratio--body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24			.362^{ns}
Anacoco	40	−3.3558	0.3003	.364*
COMBINED	64	−4.3164	0.3282	.368**

Ova diameter-body size (SL)

Locality	n	Intercept	Regression Coefficient	r
Big Cow	24	0.4200	0.0075	.443*
Anacoco	39	0.5136	0.0049	.377*
COMBINED	63	0.4735	0.0060	.409**

smaller size. Despite this complication the data are useful for a approximate comparison of size at sexual maturity in the two populations. Males matured at a smaller size than females at both localities,completing maturation by 29 mm SL in Bayou Anacoco and 30 mm SL in Big Cow Creek. Females were not completely mature until 32 mm in Bayou Anacoco and 33 mm in Big Cow Creek.

The analysis of variance performed to test for significant differences in mean size of adult males and females from Big Cow Creek indicated a significant interaction between the effects of sex and month (Table 2); therefore, a test of simple effects was performed to determine when there were differences in mean size. This procedure indicated that females were significantly larger than males in July ($p. < .05$); all other differences were non-significant. The F-value for interaction was non-significant for the Bayou Anacoco samples, as was the F-value for sex, indicating that there were no significant differences in the mean sizes of adult males and females. Significant differences between monthly

samples were indicated for both localities but were not analyzed. The results for the July sample from Big Cow Creek are unexplained; however, they may be due to sampling error. It seems reasonable to conclude that there were generally no significant differences in the mean sizes of adult males and females at either locality.

Growth and Population Age Structure

Temperatures in the study area varied considerably over short periods (daily, weekly); but mean monthly temperature variation was moderate (Fig. 3). Therefore, annulus formation in this warm temperate region is quite variable. Further, annulus formation may be especially weak for smaller individuals experiencing their first winter. Thus, scale analyses were combined with length frequency analyses to obtain the most reliable age estimates. These analyses (Figs. 8, 9) indicate that the maximum age for most *N.sabinae* is about 1½ to 2 years. None of the scales examined from March or September 1973 Big Cow Creek samples (Fig. 8; n = 50, 54, respectively) had more than two annual marks. Some specimens examined from March appeared to be forming an annulus. These data, and examinations of a few larger specimens in April and May collections (a time of active annulus formation), suggest that some of the larger individuals (particularly those 44 mm SL) may enter a fourth growing season as three-year olds. Analysis of the length

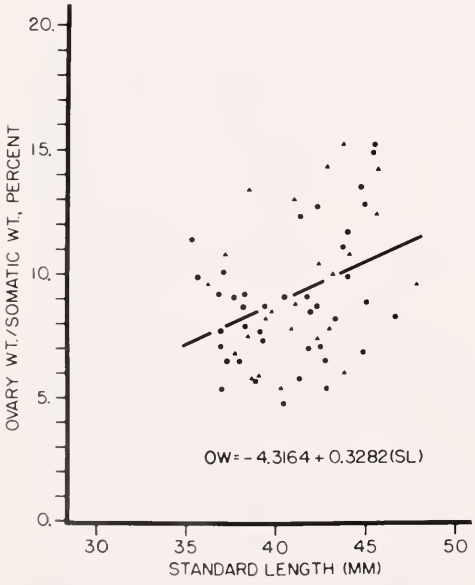

Figure 6. Relationship between ovary weight-somatic weight ratio and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

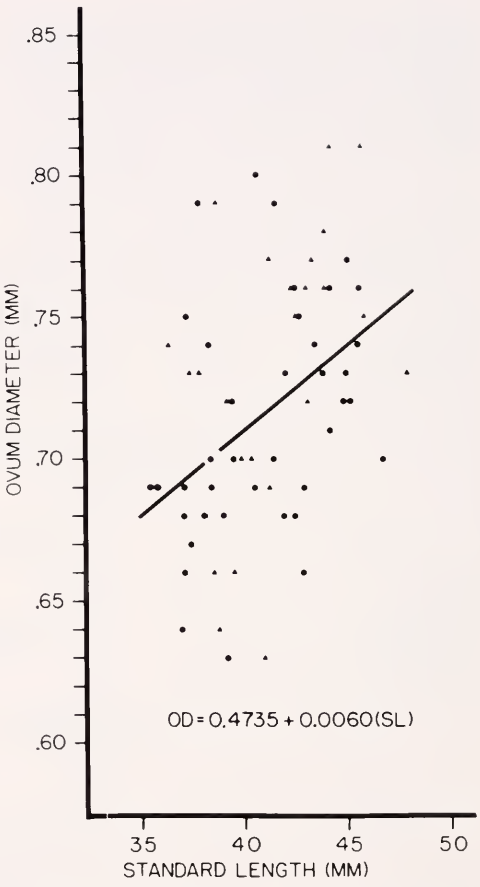

Figure 7. Relationship between mean size of unovulated, mature ova and standard length for *Notropis sabinae* females from Big Cow Creek (triangles), Texas, and Bayou Anacoco (dots), Louisiana, 1973-74 and 1976-77.

Big Cow Creek						
Sex	Date of Collection					Mean
	21 Mar 1976	2 May 1973	17 Jul 1973	21 Sep 1973	12 Oct 1973	
Male	36.834 (41)	37.225 (24)	38.673 (15)	39.796 (23)	39.943 (23)	38.5
Female	35.864 (50)	37.347 (32)	40.475 (16)	38.873 (33)	38.604 (25)	38.2

Analysis of Variance of Unweighted Means

Source	df	SS	MS	F-value
Sex	1	4.23760	4.23760	
Month	4	418.86419	104.71605	
Interaction	4	80.56889	20.14222	2.67303*
Error	272	2049.6125	7.53534	
Total	281			

Bayou Anacoco						
Sex	Date of Collection					Mean
	21 Mar 1976	2 May 1973	17 Jul 1973	21 Sep 1973	14 Nov 1973	
Male	38.670 (27)	37.942 (24)	37.782 (17)	34.929 (42)	37.053 (45)	37.3
Female	38.371 (21)	38.797 (31)	38.350 (18)	35.858 (24)	37.213 (38)	37.7

Analysis of Variance of Unweighted Means				
Source	df	SS	MS	F-value
Sex	1	12.65552	12.65552	1.66072^{ns}
Month	4	345.74802	86.43701	11.34271^{**}
Interaction	4	13.59546	3.39887	0.44602^{ns}
Error	277	2110.8763	7.62049	
Total	286			

Table 2. Mean size (mm SL), number of observations on the mean (in parentheses), and summary table for analysis of variance to test for presence of significant differences between mean size of adult (33 mm SL) male and female *Notropis sabinae* in various collections from Big Cow Creek, Texas, and Bayou Anacoco, Louisiana; ns = non-significant difference, * = significant difference at 0.05 level, ** = significant difference at 0.01 level. Adjustment of sums of squares for unequal numbers in the unweighted means analysis of variance was made to sums of squares for sex, month, and interaction.

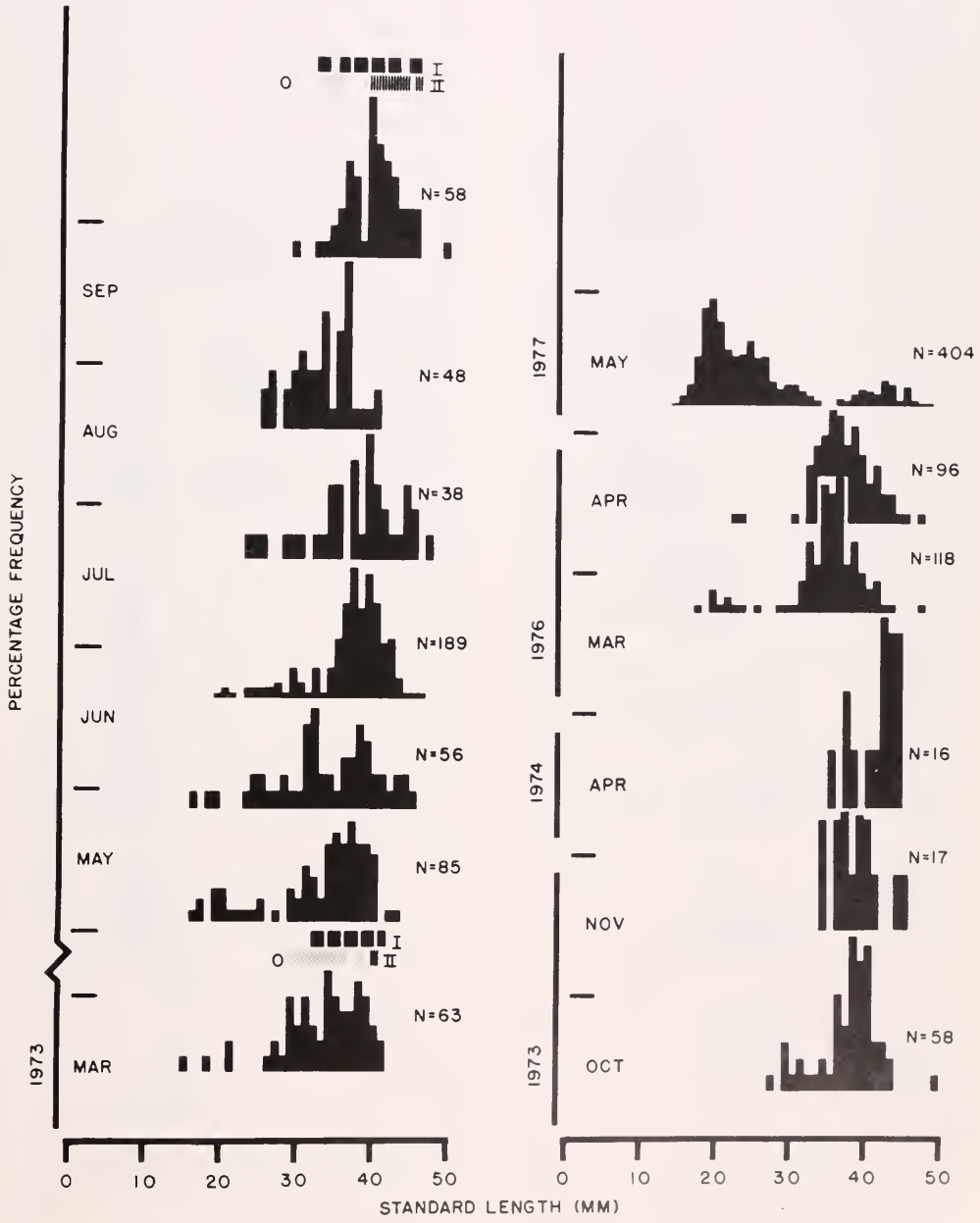

Figure 8. Length frequency histograms for collections of Notropis sabinae from Big Cow Creek, Texas. Horizontal bars are placed at beginning of each month; histogram bases are set at date of collection. Results of scale analyses are shown for March and September, 1973, collections. (0 = no annulus, I = 1 annulus, II = 2 annuli).

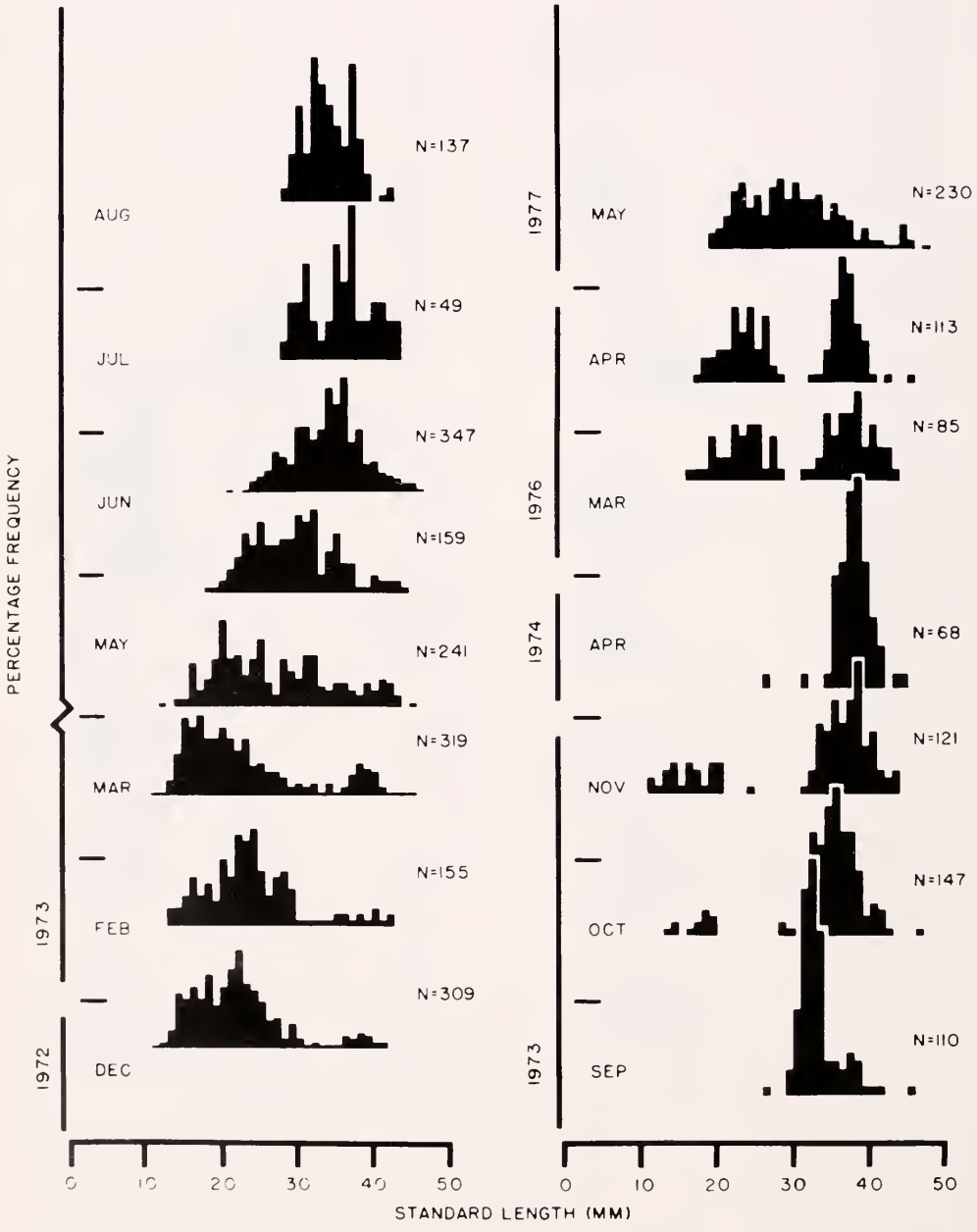

Figure 9. Length frequency histograms for collections of *Notropis sabinae* from Bayou Anacoco, Louisiana. Horizontal bars are placed at beginning of each month; histogram bases are set at date of collection.

frequency histograms for Big Cow Creek prior to and during the early part of the annual reproductive season demonstrates a bi-modal distribution. The origins and fates of these two groups suggest that the larger group is primarily comprised of one-year old individuals entering their third growth season as two-year olds. The number in this group dwindles considerably by the end of this season, suggesting that most individuals die by the age of two years. The group of smaller fish thus represents individuals having just completed a first winter and entering a second growth season as one year olds. Maximum size was about 49 mm and 47 mm SL in Big Cow Creek and Bayou Anacoco, respectively. Finally, these data and the data on size at maturity suggests that a small percentage of individuals might mature within their first growth season. However, at least the majority mature in their second season, at or within one year.

DISCUSSION

Notropis sabinae, along with other members of the *Notropis longirostris* species group (Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press), has an extended reproductive season during which it seems a number of clutches of eggs are spawned. The long annual period of high temperatures and long photoperiods in the area (Fig. 3) probably facilitates the protracted reproductive season; temperature and photoperiod are two proximal factors that activate neuroendocrine centers controlling reproductive cycles in fishes (Schwassman, 1971; DeVlaming, 1972, 1974). Nevertheless, extended reproduction may be adaptive to a variable environment in that distributing reproductive activity over a long period of time may reduce the chance of losing a large portion of the annual recruitment (Starret, 1951; Tanyolac, 1973; Wallace,, 1973; Heins and Bresnick, 1975; Heins and Clemmer, 1976; Heins et al., in press). Protracted reproduction has also been observed in a number of southern species of *Notropis* (Mathur and Ramsey, 1974; Cowell and barnett, 1974; Beach, 1974; Cowell and Resico, 1975; Heins and Bresnick, 1975).

The protracted reproductive season and presumed production of multiple clutches of eggs indicates a relatively high seasonal reproductive effort for *Notropis sabinae*. Further, *N. sabinae* is a relatively small, short-lived member of the genus *Notropis* as are other members of the *N. longirostris* species group (cf. Hubbs and Hubbs, 1958; Carlander, 1969; Snelson and Jenkins, 1973; Hubbs and Miller, 1975; Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press). *N. sabinae* also matures early, at about one year. Williams (1966) suggested that a small, short-lived species with high annual mortality should invest a greater effort in reproduction in a given season, as compared to a large, long-lived species. Additionally, strong selection for early maturity, that is within one year, should result from a short life expectancy (Tinkle, 1969).

The spawning of *N. sabinae* was not observed during this study; however, it presumably occurs over open sand as in *Notropis longirostris* (Hubbs and Walker, 1942). If this is so, *N. sabinae* would belong to the ecological guild of psammophilous fishes delineated by Balon (1975), as do other members of the *N. longirostris* species group.

Notropis sabinae, as with other members of the *N. longirostris* species group, exhibits life history traits conventionally considered characteristic of a relatively r-selected species (cf. Stearns, 1976; Balon et al., 1977). Nevertheless, some interspecific variation was observed among the life history patterns of members of the *N. longirostris* species group; variation was also noted among populations of *N. longirostris* which was more widely studied (Heins, 1979). This intra- and inter-specific life history variation will be considered in a forthcoming report. However, I will consider a distinc-

tive difference between *N. sabinae* and other members of the *N. longirostris* species group herein. Among those populations studied thus far, *N. sabinae* produces smaller mature, unovulated ova (cf. Heins and Clemmer, 1976; Heins, 1979; Heins et al., in press). The inter- and intra-specific variation observed in egg size appears to be related,at least in part, to stream flow patterns in southern North America (Fig. 10). Larger egg sizes were found in populations inhabiting areas of higher annual stream runoff (Heins, 1979). I postulate that there has been a selective advantage to larger egg size in those streams where average annual runoff is greater. Thus annual stream runoff values may indicate the relative severity of this factor in the respective stream environments. Svardson (1949) and Williams (1959) have argued that a reduction in fecundity could not be favored by natural selection unless it was a necessary consequence of some advantageous development such as increased egg size. Larger ova generally result in larger larvae that can be expected to be stronger, able to swim better, and less susceptible to damage (Blaxter, 1969). Thus, larger ova may result in larger larvae better able to survive in streams with greater average annual runoff. Heins and Clemmer (1976) had intimated this in their report on *N. longirostris*. This notion will be treated more fully along with other inter- and intra-specific variations in the life histories of members of the *Notropis longirostris* species group in a forthcoming paper.

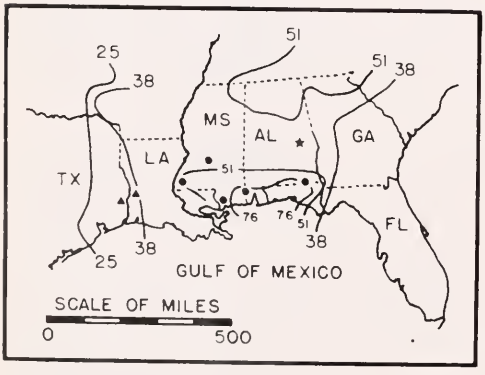

Figure 10. Map showing locations of various populations of *Notropis sabinae* (triangles), *Notropis longirostris* (dots), and *Notropis* species (cf. *N. longirostris*) (star) studied by Heins (1979) in relation to amount of annual stream runoff (cm). (After Geraghty et al. (1973), by permission.)

ACKNOWLEDGMENTS

Field sampling would have been impossible without the continued assistance of David Sever and Mike Sobczak. Gerry Bresnick, Bob Cashner, Art Johnson, Dave Myers, Pat Sorenson and Steve Stevenson also assisted with the sampling. Gerri Rehbein helped with some early laboratory analyses. My major professor, Gerald E. Gunning, has supported my research in many important ways and reviewed the original manuscript. William Dunlap aided in some statistical analyses. Mr. and Mrs. Ben P. Wilson of Call, Texas, graciously allowed me access to Big Cow Creek from their property and are deserving of special thanks. Eugene C.Beckham, III prepared the drawing of head tuberculation. Rebecca Gardner typed the manuscript. This study was supported by a Sigma Xi Grant-in-Aid of Research.

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THE SYSTEMATICS AND DISTRIBUTION OF THE HOGNOSE VIPER *BOTHROPS NASUTA*[1] BOCOURT (SERPENTES: VIPERIDAE)

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ABSTRACT

Variation in selected characters of scutellation, coloration, and body proportions in the Neotropical hognose viper, *Bothrops nasuta* Bocourt, is discussed and the speciied is redescribed. Analysis of this variation allows for the definition of three distinctive populations. No infraspecific taxa are recognized. The biogeographic history of the species is also discussed.

INTRODUCTION

Bothrops nasuta Bocourt, 1868, is a small, terrestrial pit viper occurring in humid lowland forests from Chiapas, México southward to Ecuador. It is a member of the *Bothrops lansbergi* group, a group of hognose vipers (*sensu* Burger, 1971), which was last revised by Amaral (1929a). The hognose viper group is in need of systematic study and the acquisition of an unusual specimen of *B. nasuta* from Ecuador by one of us (LP) prompted a review of the systematics of this species, the most widespread member of the group.

Amaral (1929a) had 32 specimens available to him. Since his revision more material has become available allowing for a more complete understanding of the systematics of this species.

MATERIAL AND METHODS

We examined 241 specimens of *Bothrops nasuta*. The single specimen of this species from Belize (Neill, 1965) was not available to us. The following scales were counted using the definition of Klauber (1972): intercanthals, prefoveals, preoculars, suboculars, and postoculars. We follow Burger (1971), with some modification, in defining and recording the following scales: postcanthals, interictals, interoculars, oculabials, and nasorostrals. The definitions of these latter scales are as follows:

Postcanthals. The undifferentiated marginal head scale(s) contacting the upper preocular between the canthal and supraocular.

Interictals. The supracephalic scales occupying the posterior portion of the head from oral rictus to oral rictus. For consistency, the interictals were counted between the last supralabials.

Interoculars. The irregularly disposed scales in the frontal region that were counted along the path between the supraoculars that traverses the fewest scales.

Oculabials. The rows of scales between

[1]According to Shreve (1957), Amaral (1964a, 1964b, 1976) and Schwartz and Thomas (1975), generic names ending in *-ops* are feminine in classical Greek usage. Thus, the specific name for this hognose viper is *nasuta*, not *nasutus*. For opinions to the contrary, see the 1964 edition of the International Code of Zoological Nomenclature and Smith and Larsen (1974).

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suboculars and supralabials but including neither.

Nasorostrals. The scales between the nasal and rostral.

The number of ventral scales was counted using the method of Dowling (1951). Due to the irregularity of scutellation in the nasofrontal area, the scales anterior to and including the interoculars, except for those bordering the edge of the head (rostral, internasals, canthals, postcanthals, and supraoculars), were counted and given the name nasofrontals. Postfoveals and median gulars were not counted due to their high degree of variability and consequent difficulty of accurate tabulation. The dorsal scale rows were counted one head length posterior to the interictals, at midbody, and at the vent. All measurements were made on preserved specimens, with the exception of those made on a record-length specimen from Ecuador in the senior author's live collection.

Statistical analyses were accomplished using the Student's *t* test, as described by Simpson, et al. (1960), using a probability value of .95.

Inasmuch as *Bothrops nasuta* has a basically linear distribution, we used, for the sake of convenience, the political boundaries within the animal's range as the basis for subdividing for analysis our data on variation. The populational groupings in the tables are defined in the discussion.

HISTORICAL SUMMARY

A considerable amount of confusion has existed in the literature concerning the hognose vipers. Much of the confusion was largely eliminated by Amaral's paper (1929a) on the *Bothrops lansbergi* group. In that paper Amaral redescribed *Bothrops nasuta* Bocourt and demonstrated its distinctness from *B. lansbergi* (Schlegel). He also snyonymized *B. brachystoma* (Cope) with *B. lansbergi*, thus terminating the application of the name *brachystoma* to specimens of *B. nasuta*. Moore (1962), however, incorrectly placed *brachystoma* as a synonym of *B. nasuta*.

Cope (1876) described *Bothriopsis proboscideus*. Later, he (1879) questioned the validity of *B. proboscideus* but continued to recognize it in a later paper (Cope, 1887). Amaral (1929a) placed *B. proboscideus* in the synonymy of *Bothrops nasuta*.

Posada-Arango (1889a) proposed a new genus of solenoglyph snakes, *Thanatos*, and described several new species, including *T. sutus*. Later in the same year (1889b) he introduced the generic name *Thanatophis*, without explanation (*fide* Vanzolini, 1977). Nicéforo María (1938) concluded that *Thanatophis sutus* is probably a synonym of *Bothrops nasuta*. His decision was tentative due to Posada-Arango's generalized description. García (1896), using the nomenclature of Posada-Arango, figured a specimen identified as *Thanatophis sutus*, which is actually a juvenile *B. nasuta*, supporting the contention that the two names are synonymous, a supposition supported by Daniel (1949, 1955), Burger (1971), and us. Peters and Orejas-Miranda (1970) and Vanzolini (1977) incorrectly place *Thanatophis* (or *Thanatos*) *sutus* as a synonym of *Bothrops lansbergi*.

Burger (1971) subdivided the various members of the genus *Bothrops* (*sensu lato*) into five genera. *Bothrops nasuta* was placed in the genus *Porthidium* as *P. nasutum*. This disposition was accepted by Smith and Smith (1976). Whereas we are in fundamental agreement with the generic limits proposed by Burger (1971), we prefer not to use them inasmuch as an adequate analysis of the basis for such a classification was not presented by him. In addition, Burger (1971) recognized two subspecies, *nasutum* and *sutum* (=*nasuta* and *suta*). This disposition was unsupported with any data and is not followed by us (see analysis of variation).

SPECIES ACCOUNT

Bothrops nasuta Bocourt

Bothrops lansbergii: Günther, 1863: 350; Dunn, 1928: 30 (part); Picado.1936: 392; E. H. Taylor, 1951: 178, 1954: 681.

Bothrops nasutus Bocourt, 1868: 202 (type locality: Panzós, on the banks of the Río Polochic, Guatemala; holotype: MNHN 1592 - *fide* Stuart, 1963), 1876: 410; Barbour and Loveridge, 1929: 3; Smith, 1943: 400, 1958: 224; Smith and Taylor, 1945: 182; Stuart, 1948: 87, 1950: 24, 1958: 29, 1963: 130; E. H. Taylor, 1954: 783; Moore, 1962: 62; Duellman, 1963: 245, 1966: 705; Klemmer, 1963: 408; Neill, 1965: 113; Hoge, 1965: 127; Savage, 1966: 751, 1973: 17; Heyer, 1967: 267; Moore, et al., 1968: 48, 61; Meyer, 1969: 415; Minton and Minton, 1969: 207; Scott, 1969: 232; Peters and Orejas-Miranda, 1970: 49; Hoge and Romano, 1971: 252; Alvarez del Toro, 1973: 158; R. T. Taylor et al., 1974: 384, 388; Henderson and Hoevers, 1975: 51; Campbell, 1976: 153.

Porthidium nasutus: Cope, 1871: 207.

Porthidium nasutum: Cope, 1871: 207, 1876: 151, 1879: 271, 1887: 89; Smith and Smith, 1976: S-B-16.

Bothriopsis proboscideus Cope, 1876: 150 (type locality: Sipurio, at base of mountains, Costa Rica; no holotype designated); Cope, 1879: 271.

Bothrops lansbergi: Müller, 1878: 703 (in error).

Bothrops brachystoma: Müller, 1882: 154; Amaral, 1925: 29, 1927a: 22, 1927b: 47; Loveridge, 1928: 63.

Bothriopsis (sic) *proboscideus*: Cope, 1887: 89.

Brothriopsis brachystoma: Cope, 1887: 89 (part).

Thanatos sutus Posada-Arango, 1889a: 45-49 (paper not seen).

Thanatophis sutus Posada-Arango, 1889b: 344 (type locality: "le district de Zea," Colombia; no holotype designated); García, 1896: 26.

Bothriechis lansbergii: Gunther, 1895: 190 (part).

Lachesis brachystoma: Boulenger, 1896: 547 (part); Boettger, 1898: 139.

Trimeresurus brachystoma: Mocquard, 1909, 945 (part).

Bothrops nasuta: Amaral, 1929a: 25. 26, 1929b: 237, 1931a: 89, 1931b: 94, 1935: 22, 1944a: 7, 10, 1944b: 18; Picado, 1931a: 69, 1931b: 104, 1936: 391; Dunn and Emlen, 1932: 32; Dunn, 1933: 79, 1944: 215; Schmidt, 1933: 19; Wettstein, 1934: 38; Nicéforo Maria, 1938: 419, 1942: 101; Prado, 1939: 1; Rendahl and Vestergren, 1941: 16, Daniel, 1949: 329, 1955: 80; Pifano and Römer, 1949: 302; E. H. Taylor, 1951: 177; Peters, 1960: 510; Villa, 1962: 50; Brattstrom 1964: 189; Medem, 1968: 194; Minton and Minton, 1969: 216; Wilson and Meyer, in press.

Trimeresurus nasutus: Dunn and Bailey, 1939: 20; Smith, 1941: 62.

Porthidium nasutum nasutum: Burger, 1971: 35, 132.

Porthidium nasutum sutum: Burger, 1971: 35, 132.

Description - The scutellation of this species is as follows: rostral higher than wide, the ventrolateral portion infrequently separated off as a nasorostral (5.0% of specimens examined); internasals paired, elongate, elevated anteriorly, usually in contact (81.4%); canthals usually single (96.6%); postcanthals often one (67.7%), sometimes two; intercanthals 3-7 (x=4.95); nasofrontals 20-59 ($\bar{x}$=37.23); interoculars 3-7 ($\bar{x}$=5.19); lateral edge of supraoculars flattened; interictals 19-28 ($\bar{x}$=24.58); nasal scale partially divided; prefoveals 2-12 ($\bar{x}$=5.60); subfoveals 1-7 ($\bar{x}$=2.26); loreal wider than high, upper preocular large, extending dorsally over the canthal ridge; middle preocular divided or not, infrequently absent, in contact with orbit or not; lower preocular single, in-

frequently absent, in contact with orbit or not; suboculars 1-4 ($\bar{x}$=1.66); postoculars 1-4 ($\bar{x}$=2.30); oculabials 1-4, usually 2 (88.8%); supralabials 8-11 ($\bar{x}$=9.34); infralabials 9-13 ($\bar{x}$=11.41), the first pair usually in contact; a single pair of chinshields; ventrals 123-145 ($\bar{x}$=135.80); anal plate single; subcaudals entire, 24-41 ($\bar{x}$=30.02); tail not prehensile; dorsal scale rows at neck 23-29, usually 25 (87.8%), at midbody 21-27, usually 23 (92.8%), at vent 17-21, usually 19 (96.6%); apical pits absent.

The hemipenis is divided with a bifurcate sulcus spermaticus, the sulcus dividing close to the base of the organ and each branch extending to the distal end of the apical lobe. The basal portion of the organ and the areas lateral to and between the branches of the sulcus are spinulate. The shoulders and the absulcate side of the organ are covered with spines which increase gradually in size proximally, terminating with a pair of enlarged basal spines situated on either side of the sulcus. Distal areas of the apical lobes are calyculate with papillate micro-ornamentation.

Distribution and Ecology - *Bothrops nasuta* is an inhabitant of the humid lowlands of Middle America and adjacent northwestern South America (Figs. 1 and 2). *Bothrops nasuta* belongs to the Eatern Mesoamerican Complex of Savage (1966) and the Humid Tropical Assemblage of Duellman (1966). It is distributed along the Caribbean lowlands from northern Chiapas, México, eastward through northern Guatemala, possibly to Belize (see discussion below), thence southward through Central America (Fig. 1) and onto the Pacific coastal plain of western Columbia to midwestern Ecuador (Fig. 2). The species probably also occurs in the mesic lowlands of eastern Veracruz, México, inasmuch as it has been recorded near the border in Chiapas in the same type of forest (Alvarez del Toro, 1973). A specimen (ANSP 4873) recorded from "Veracruz, Mexico" shows characters of specimens from much farther south in the range and we regard the data as questionable. The species probably also occurs in the southern portions of Tabasco.

The occurrence of *Bothrops nasuta* in Belize is questionable. Schmidt (1941) recorded a specimen of a hognose viper from Benque Viejo, Cayo District, Belize, which he identified as *Trimeresurus yucatanicus*. Neill (1965) recorded a specimen of *B. nasuta* from Xuantunich (=Benque Viejo), Cayo District, and speculated that Schmidt's specimen was probably of the latter species. This disposition was followed by Henderson and Hoevers (1975). McCranie and Porras (1978) examined the Schmidt specimen (USNM 61781), however, and determined it to be *Bothrops yucatanica*, thus reestablishing the occurrence of this species in Belize. The description of the specimen reported by Neill (1965) is ambiguous and will not distinguish *B. nasuta* from *B. yucatanica*.

In the northern part of its range (the Mexican and most of the Guatemalan portion), *B. nasuta* lives in the broadleafed forest or quasi-rainforest division of the evergreen forest (c.f. Duellman, 1966; also see Stuart, 1966). Duellman (1966) characterized these forests as having a marked dry season at which time some of the trees become leafless. However, some rain apparently falls throughout the year (Duellman, 1963). Stuart (1958) considered the forests of El Petén, Guatemala, as representing a transition from the wet forests of the south and the dry forests of the outer Yucatán Peninsula to the north. *Bothrops nasuta* apparently adapts to the drier conditions of the quasi-rainforest by living in thick woods around marshy areas (Alvarez del Toro, 1973), in the vicinity of rivers where the forests are more mesic (Chamá, 12 km NW Chinajá, Panzós, Piedras Negras, and Sayaxché, Guatemala), under similar conditions around Lago Miramar, Chiapas, México, and in the high forests surrounding the *aguadas*

of the Petén region of Guatemala. From extreme eastern Guatemala southward throughout Central America, the range of *B. nasuta* is within the more humid tropical rainforest division of the evergreen forest (c.f. Duellman, 1966). This forest differs from the quasi-rainforest in that the habitat is at least moderately moist throughout the year even though rainy and dry seasons are evident. These moist conditions are enhanced by the tendency of the forest to develop a continuous treetop canopy which provides abundant shade creating the "greenhouse effect" discussed by Duellman (1966). The only known occurrence of *B. nasuta* outside the evergreen forest is in the scrub forest (c.f. Duellman, 1966) of the Sula Plain near San Pedro Sula, Honduras. However, we believe these specimens came from gallery forest associated with the rivers of the region.

In several places in Costa Rica and Panamá, *Bothrops nasuta* crosses the Continental Divide onto the Pacific versant. The species has been collected on both sides of the divide in the Tilarán area of Guanacaste Province, Costa Rica. Along the Tilarán transect studied by heyer (1967), the range of *B. nasuta* is apparently continuous across the low divide (850 m) onto the Pacific versant, where the species has been collected approximately 4 km west of the divide. One

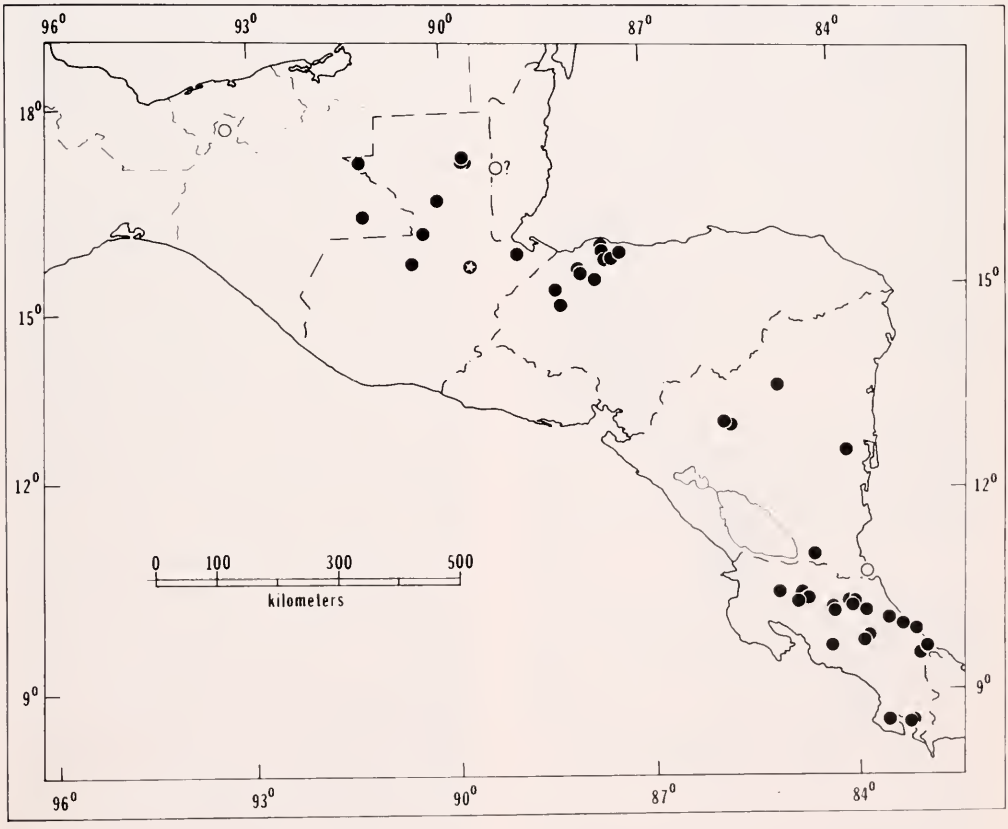

Figure 1. Distribution of *Bothrops nasuta* in Central America. Solid symbols represent localities of specimens examined. Hollow circles represent literature records (see section on distribution and ecology for discussion of questioned locality in Belize). The type locality is indicated by a star within a circle.

specimen (UCR 110) was collected on the Pacific versant at Puriscal (=Santiago), San José Province, Costa Rica. This specimen represents a relict population. An isolated population also occurs on the Pacific lowlands of the Golfo Dulce area of Costa Rica and probably adjacent Panamá. Savage (1966) and Savage and Vial (1974) discussed the factors creating the isolation of the vegetation of this region. However, the herpetofauna of the Golfo Dulce area resembles that of the Caribbean lowlands of Costa Rica and Panamá (Duellman, 1966; Savage, 1966; Savage and Vial, 1974). In Panamá, *B. nasuta* has been collected on the Pacific versant close to the Continental Divide in El Valle de Antón, Coclé Province. Dunn (1933), in a discussion of the El Valle area, stated that "Atlantic side conditions and fauna come a little way over the divide onto the Pacific versant." Two specimens collected by Herbert Clark (MCZ 37115-16) are recorded from Panama City, Panamá. Panama City is located in a savanna habitat (c.f. Duellman, 1966). These two specimens probably came from farther north in the mesic forests of the Canal Zone area where Clark obtained 13 other specimens. No specimens are available from Panamá east of the Canal Zone area, but it undoubtedly occurs in the Caribbean mesic forests of eastern Panamá.

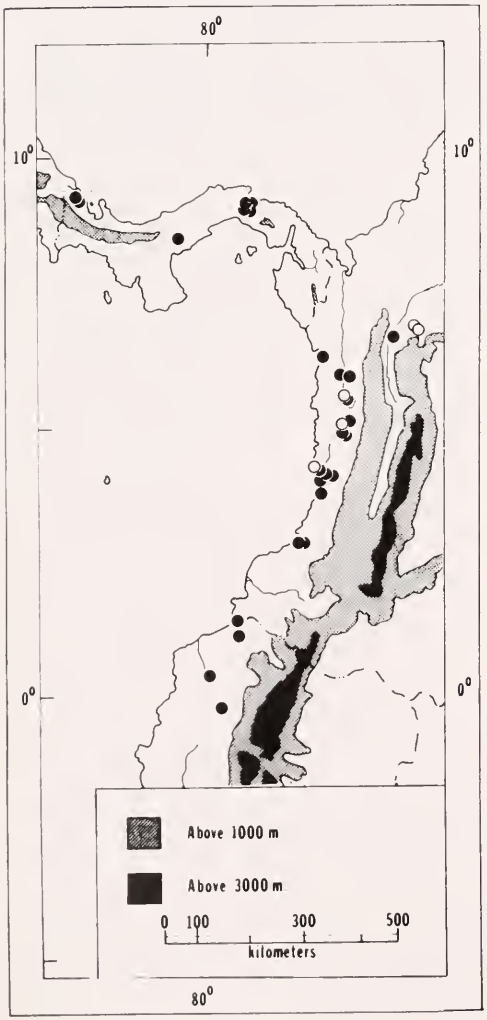

Figure 2. Distribution of *Bothrops nasuta* in Pananá, Colombia, and Ecuador. For explanation of symbols see Figure 1.

In South America *Bothrops nasuta* inhabits the lowland rainforests of Colombia west of the Andes southward to midwestern Ecuador. Dunn (1940), Duellman (1966), and Savage (1966) discussed the "crossover effect" occurring in the eastern Panamá-northwestern Colombia region, where the Caribbean mesic forms of lower Central America cross onto the wet Pacific lowlands of Colombia. However, the Pacific lowlands consist of a very narrow strip in northwestern Colombia. The lowland rainforests east of the Andes in the central portion of the department of Chocó and the adjacent western part of the department of Antioquia, Colombia, which are also inhabited by *B. nasuta*, are drained by the Río Atrato and its tributaries, which then flow northward into the Caribbean Sea. It is not until the Río San Juan drainage of southern Chocó is reached that *B. nasuta* becomes essentially a Pacific coastal plain animal, which it then remains to the terminus of its range in midwestern Ecuador. *Bothrops nasuta* also inhabits the low-

land rainforests of the rios Cauca and Porce in the department of Antioquia, Colombia. As with the Río Atrato, these latter two rivers flow northward into the Caribbean. The forests along the eastern edge of the Andes and on the Pacific coastal plain of Colombia are one of the most humid areas of the world and certainly the most humid of all of South America (Eidt, 1968; Haffer, 1970). The rains in the Quibdó area, Chocó, Colombia, fall year around (Haffer, 1970). Eidt (1968), in describing central Chocó, Colombia, stated that "only for a few days each year, usually when winds from the north disturb the general calm of the region, are there brief respites from the near constant rains." Myers et al. (1978) discussed the habitat at Quebrada Guanguí, Depto. Cauca, Colombia, where they collected a series of *B. nasuta* (AMNH 109794-811).

Bothrops nasuta occurs from near sea level to about 900 m in elevation, but is generally found below the 600 m contour. Of 112 specimens with elevational data, 49 (43.8%) were from below 200 n and 107 (95.5%) were from below 625 m The highest elevation datum available i 900 m for two specimens (UMMZ 116523, 117735) from near Matagalpa Nicaragua. Dunn (1944) gave an eleva tion of 1885 m for *B. nasuta* based on a record for Urrao, Antioquia, Colombia (Nicéforo María, 1938, 1942). We doubt that the specimen actually came from this elevation. Nicéforo Maria (1938) stated "que le fueron remitidos de. . .." This literally means "received from," which we interpret to mean "shipped from." We also question two other Nicéforo María (1938, 1942) records; Pueblo Rico, Depto. Caldas and Medellín, Depto. Antioquia. The elevations of these last two places are 1500 and 1538 m, respectively (Medem, 1965). Of 24 Colombian specimens with elevational data, all were from 200 m or below.

Bothrops nasuta is both terrestrial and nocturnal, although specimens can be found sunning themselves by day (Smith, 1943; pers. observ.). The species can also be found on low bushes or shrubs (E. H. Taylor, 1954; Medem, 1968). Posada-Arango (1889b) mistakenly believed that *B. nasuta* is arboreal, as did Amaral (1927b), when he said that *B. brachystoma* (=*B. nasuta*) "is a tree viper." Specimens have been found inside cavities in the trunks of trees, underneath roots of trees or rocks, on top of piles of rubbish (Alvarez del Toro, 1973), under rotting logs (Stuart, 1958), inside huts (Stuart, 1948), among loose rocks of ruins, (Smith, 1943), or simply on the forest floor (Duellman, 1963). We have collected *B. nasuta* under and lying near logs in the Turrialba area of Costa Rica.

Picado (1931a) reported that newborn *Bothrops nasuta* will eat earthworms and later will consume small lizards of the genus *Anolis*. Amaral (1927b) stated that the species feeds on lizards and Alvarez del Toro (1973) indicated that it feeds on anoles and mice. Picado (1931a) reported an instance of cannibalism involving juveniles. We have observed cannibalism among adults and juveniles in captivity. We have also observed them to eat leopard frogs (*Rana* sp.), anoles (*Anolis* sp.), and mice in captivity.

Bothrops nasuta has been reported to have 8 to 18 young (Picado, 1931a). A specimen in our collection (now LSUMZ 36898) from near Turrialba, Costa Rica, gave birth to 14 young in September, 1967.

Bites from *B. nasuta* are known to cause fatalities in human beings (Daniel, 1949), although Minton and Minton (1969) did not believe they are capable of doing so.

ANALYSIS OF VARIATION

Twenty-six characters were analyzed for geographic, sexual, ontogenetic, and individual variation. These characters are discussed below.

Internasals. - Typically, *Bothrops*

nasuta has the internasal scales in medial contact or separated by only one scale. One specimen (FMNH 68056), however, has the internasals separated by two scales. This specimen also has one shortened and one elongate internasal scale. Two specimens (LACM 45413, 45416) from Colombia do not have the internasal scales as elevated as do other *B. nasuta*, but are typical in all other respects.

The frequency of medial contact of the internasals varies geographically. All of the specimens of *B. nasuta* from México southward to Nicaragua have their internasals in mutual contact. Three specimens from Costa Rica and one from adjacent northwestern Panamá have their internasal scales separated by one scale, but two of these specimens are from the Península de Osa. The frequency of the mutual internasal contact is reduced in specimens from central Panamá southward to Ecuador (Table 1). In addition, specimens from central Panamá and Ecuador have the internasals in contact less frequently than do specimens from Colombia. In all of the specimens but one, which is a juvenile, from the Península de Osa, the internasals are less elevated and the snout is more attenuate.

Nasofrontals. - The numbers of nasofrontal scales in male *B. nasuta* average slightly lower than in females (Table 2) but the differences are not statistically significant.

Specimens from central Panamá exhibit a high average number of nasofrontal scales relative to other areas of the range (47.21 ± 2.63 as opposed to 37.79 ± 0.89).

Intercanthals. - Males average fewer intercanthals than do females (Table 3), except in central Panamá, but the latter differences will probably be reversed with study of additional material.

Central and western Panamanian specimens have a higher average number of intercanthals than do specimens from the remainder of the range (5.48 ± 0.36 vs. 4.92 ± 0.10).

Interoculars. - The average number of interoculars is higher in females than in males in the entire sample but the differences are not statistically significant (Table 3). However, specimens from the northern portion of the range (western Panamá northward), excepting the Península de Osa, show no statistically significant average difference between the sexes, whereas those from that point southward do (Table 3).

Interictals. - Generally, males have fewer interictals than do females but the differences are not statistically significant (Table 3).

Rostral. - Two specimens (AMNH 10981, UMMZ 91078) have the rostral scale horizontally divided. All other specimens have a single rostral scale.

Nasorostral. - A nasorostral scale is occasionally present in specimens from disparate parts of the range. The incidence of females possessing this scale appears to be greater than that of the males, inasmuch as ten of the twelve specimens having 1 or 2 nasorostrals are females.

Nasal. - All specimens of *B. nasuta* examined have a partially divided nasal scale, except for two, which have the scale completely divided. The usual condition is that of a partial crease at the upper and lower sections of the scale but a few specimens exhibit a complete division of this scale above or below the naris.

Prefoveals. - One specimen (UMMZ 117735) has the prefoveal scales extending to the rostral scale thus excluding the nasal scale from contact with the first supralabial.

Females have more prefoveals on the average than do males throughout the range (Table 4).

Subfoveals. - With respect to the sample as a whole, males have significantly fewer subfoveals than do females (Table 4).

Preoculars. - There are generally an upper, middle, and a lower preocular

Table 1. Variation in internasals, body blotches, and sex ratios in Bothrops nasuta (parenthetical numbers in first and last columns indicate sample size; middle columns indicate range, mean, confidence limits, and sample size, where applicable)

	Internasals	Body blotches		Sex ratios
	% in contact	Males	Females	% of females
México	100(2)	-	17	100(2)
Guatemala	100(13)	18-22(19.29±1.16)7	15-17(15.75±0.74)8	61.1(18)
Honduras	100(16)	17-20(18.50±19.06)2	15-18(15.88±0.94)8	81.3(16)
Nicaragua	100(7)	17-19(17.67±2.88)3	16	57.1(7)
Costa Rica	98.9(95)	16-22(18.36±0.63)25	15-20(17.22±0.48)36	60.0(95)
Western Panamá	90.0(10)	19-22(20.00±4.30)3	16-19(18.20±1.04)5	70.0(10)
(Northern Population)	98.6(148)	16-22(18.60±0.49)40	15-20(16.90±0.33)60	63.5(148)
(Osa Population)	71.4(7)	18-20(19.0±12.71)2	15-19(16.67±5.18)3	57.1(7)
Central Panamá	22.2(18)	19-23(19.00±4.68)4	16-19(17.77±0.70)13	78.9(19)
Colombia	66.7(57)	15-23(19.31±0.77)26	15-22(18.61±0.66)25	52.6(57)
Ecuador	22.2(9)	17-20(19.00±1.52)5	17-18(17.75±0.80)4	44.4(9)
(Southern Population)	52.4(84)	15-23(19.23±0.66)35	15-22(18.26±0.45)42	57.6(85)
Totals	81.6(239)	15-23(18.90±0.39)77	15-22(17.44±0.29)105	61.3(240)

(95.0% of the specimens examined). The contact of the preoculars with the orbit is inconsistent, expecially since there is often a fleshy rim of tissue interposed between the preoculars and the orbit. Individual specimens exhibit different preocular arrangements on either side of the head. There are occasional specimens that do not have a middle preocular. This condition usually occurs when the upper and lower preoculars are enlarged and in contact with each other, thus excluding the middle one from orbital contact. In one specimen (MCZ 55069) an enlarged supralacunal takes the place of the middle preocular.

Suboculars and Postoculars. - The subocular and postocular scales vary in number (see description). In many specimens counts varied widely from one side of the head to the other. Specimens had as few suboculars as one or as many as four and postoculars range from two to four on either side of the head of the same animal.

Oculabials. - The usual number of oculabials present in *B. nasuta* is two (88.8% of specimens examined).

Male *B. nasuta* from the entire range have significantly fewer oculabial scales than do females (Table 5).

The number of specimens in which the

Table 2. Variation in ventrals, subcaudals, and nasofrontals in Bothrops nasuta (parenthetical numbers indicate range, mean, confidence limits, and sample size, where applicable)

	Ventrals		Subcaudals		Nasofrontals	
	Males	Females	Males	Females	Males	Females
México	-	138	-	29-30(29.50±6.35)2	-	28-32(30.00±25.41)2
Guatemala	138-141(139.14±0.99)7	140-145(142.27±1.09)11	34-38(35.57±1.17)7	28-32(29.64±0.16)11	26-39(31.14±3.80)7	29-43(37.18±3.59)11
Honduras	135-139(137.33±5.17)3	135-142(139.67±1.47)12	33-35(34.33±2.88)3	26-30(27.91±0.70)11	26-46(36.00±127.06)2	29-48(34.92±3.52)12
Nicaragua	139-142(140.33±3.80)3	136-140(138.50±2.76)4	28-33(30.50±31.77)2	27-29(28.00±1.84)4	33-35(33.67±2.87)3	32-46(38.50±9.23)4
Costa Rica	129-143(136.37±0.84)38	128-144(137.35±0.42)57	27-41(32.67±0.72)36	24-35(28.46±0.18)54	22-43(33.53±1.69)38	25-54(35.05±1.54)56
Western Panama	133-138(136.00±6.60)3	129-139(135.29±3.65)7	34-36(35.00±2.48)3	25-31(27.86±1.63)7	39-42(41.00±4.30)3	33-46(40.86±4.61)7
(Northern Population)	129-143(136.98±0.71)54	128-145(138.14±0.55)92	27-41(33.22±0.65)51	24-35(28.49±0.46)89	22-46(33.77±1.48)53	25-54(35.78±1.20)92
(Osa Population)	136-137(136.67±1.43)3	136-139(137.25±2.39)4	33(33.00±0)2	25-27(26.25±1.52)4	20-34(28.33±12.95)3	33-40(36.25±4.75)4
Central Panamá	129-131(130.25±1.52)4	130-139(134.47±1.34)13	30-34(31.00±3.18)4	26-32(28.86±0.96)14	38-53(48.18±10.43)4	39-59(46.90±2.93)15
Colombia	123-141(130.54±1.37)26	127-143(132.83±1.31)29	28-35(32.00±0.60)27	24-31(28.07±0.59)30	25-56(39.22±3.37)27	29-58(41.43±2.56)30
Ecuador	127-137(131.00±4.65)5	132-136(133.50±3.05)4	31-35(33.00±1.96)5	28-29(28.50±0.92)4	32-44(39.20±5.72)5	31-45(40.25±10.18)4
(Southern Population)	123-141(130.57±1.10)35	127-143(133.35±0.92)46	28-35(32.03±0.55)36	24-32(28.33±0.45)48	25-56(40.14±2.77)36	29-59(42.84±1.92)49
Totals	123-143(134.53±0.28)92	127-145(136.56±0.58)142	27-41(32.73±0.44)89	24-35(28.38±0.33)141	20-56(36.09±1.54)92	25-59(38.17±1.12)145

Table 3. Variation in intercanthals, interoculars, and interictals in Bothrops nasuta (explanations as for Table 2)

	Intercanthals		Interoculars		Interictals	
	Males	Females	Males	Females	Males	Females
México	-	5(5.00±0)2	-	4-6(5.00±12.71)2	-	25-27(26.00±12.71)2
Guatemala	4-5(4.43±0.47)7	5-6(5.09±0.20)11	5-6(5.29±0.45)7	3-6(4.55±0.63)11	23-26(24.86±0.83)7	23-26(25.09±0.70)11
Honduras	4-5(4.33±1.40)3	4-6(4.92±0.46)13	3-5(4.33±2.87)3	3-7(4.31±0.71)13	25-27(25.67±2.87)3	23-27(24.85±0.73)13
Nicaragua	5(5.00±0)3	5-6(5.50±0.92)4	5(5.00±0)3	5-7(6.00±1.30)4	23-25(24.00±2.48)3	24-27(25.50±2.05)4
Costa Rica	3-6(4.53±0.23)38	4-7(4.89±0.15)57	4-7(5.21±0.26)38	3-7(5.35±0.20)57	19-27(24.00±0.53)38	19-28(24.51±0.41)57
Western Panamá	4-6(5.00±2.48)3	5-7(5.71±0.88)7	5-7(6.33±2.87)3	5-7(5.86±0.34)7	23-24(23.33±1.43)3	22-26(24.29±1.16)7
(Northern Population)	3-6(4.56±0.18)54	4-7(5.01±0.13)94	3-7(5.22±0.23)54	3-7(5.17±0.20)94	19-27(24.17±0.41)54	19-28(24.68±0.29)94
(Osa Population)	3-5(4.00±2.48)3	4-6(4.75±1.52)4	4-5(4.67±1.43)3	5-7(6.00±1.30)4	25(25.00±0)3	25-27(26.25±1.52)4
Central Panamá	5-7(5.75±1.52)4	3-7(5.40±0.55)15	4-5(4.75±0.80)4	5-7(5.47±0.35)15	22-25(23.75±2.00)4	22-25(24.33±0.50)15
Colombia	4-7(5.11±0.32)27	4-7(5.47±0.32)30	3-7(4.70±0.42)27	4-7(5.30±0.28)30	22-26(24.04±0.46)26	22-27(24.87±0.42)30
Ecuador	4.5(4.60±0.68)5	5-6(5.25±0.80)4	5(5.00±0)5	6-7(6.50±0.92)4	24-27(25.60±1.41)5	24-26(25.50±1.59)4
(Southern Population)	4-7(5.11±0.28)36	3-7(5.43±0.25)49	3-7(4.75±0.32)36	4-7(5.45±0.22)49	22-27(24.23±0.43)35	22-27(24.76±0.31)49
Totals	3-7(4.75±0.16)93	3-7(5.14±0.12)147	3-7(5.02±0.18)93	3-7(5.29±0.18)147	19-27(24.22±0.29)92	19-28(24.75±0.22)147

Table 4. Variation in prefoveals, subfoveals, and postcanthals in Bothrops nasuta (explanations as for Table 2).

	Prefoveals		Subfoveals		Postcanthals	
	Males	Females	Males	Females	Males	Females
Mexico	-	3-6(5.00±2.25)2	-	2-3(2.75±0.80)2	-	1(1.00±0)2
Guatemala	3-4(3.14±0.21)7	4-8(5.73±0.46)11	1-3(2.00±0.23)7	2-4(2.36±0.26)11	1(1.00±0)7	1-2(1.18±0.26)11
Honduras	3-8(4.80±2.39)3	4-9(6.00±0.50)13	2-3(2.40±0.68)3	2-5(2.62±0.29)13	1(1.00±0)3	1-2(1.08±0.55)13
Nicaragua	4-8(6.17±1.40)3	5-11(8.13±1.92)4	1-2(1.67±0.54)3	2-7(3.38±1.48)4	1-2(1.17±0.43)3	1-2(1.38±0.43)4
Costa Rica	2-9(4.62±0.35)37	3-12(6.11±0.28)57	1-4(2.09±0.14)37	1-5(2.42±0.14)57	1-2(1.14±0.08)37	1-2(1.61±0.09)57
Western Panama	5-7(6.17±0.79)3	4-10(6.64±1.00)7	2-3(2.33±0.54)3	2-4(2.29±0.35)7	1(1.00±0)3	1-2(1.79±0.25)7
(Northern Population)	2-9(4.61±0.30)53	3-12(6.15±0.22)94	1-4(2.09±0.11)53	1-7(2.48±0.11)94	1-2(1.10±0.06)53	1-2(1.47±0.07)94
(Osa Population)	3-8(4.67±0.96)3	3-7(5.00±1.09)4	1-3(2.00±0.66)3	2-3(2.13±0.37)4	1(1.00±0)3	1-2(1.25±0.39)4
Central Panama	5-8(6.13±1.13)4	3-11(6.23±0.78)15	1-3(2.13±0.54)4	1-3(1.97±0.11)15	1-2(1.50±0.45)4	1-2(1.43±0.19)15
Colombia	3-9(4.96±0.42)27	3-11(6.27±0.45)30	1-3(2.09±0.13)27	1-5(2.38±0.17)30	1-2(1.07±0.07)27	1-2(1.30±0.12)30
Ecuador	3-5(3.90±0.53)5	5-8(6.50±0.89)4	1-3(2.00±0.48)5	1-3(1.88±0.54)4	1-2(1.20±0.37)5	1-2(1.25±0.16)4
(Southern Population)	3-9(4.94±0.36)36	3-11(6.28±0.36)49	1-3(2.08±0.12)36	1-5(2.21±0.14)49	1-2(1.14±0.08)36	1-2(1.34±0.10)49
Totals	2-9(4.74±0.22)92	3-12(6.16±0.19)147	1-4(2.08±0.08)92	1-7(2.38±0.09)147	1-2(1.11±0.05)92	1-2(1.42±0.06)147

Table 5. Variation in supralabials, infralabials, and oculabials in Bothrops nasuta (explanations as for Table 2).

	Supralabials		Infralabials		Oculabials	
	Males	Females	Males	Females	Males	Females
Mexico	-	10-11(10.25±0.80)2	-	12-13(12.25±0.80)2	-	2(2.00±0)2
Guatemala	9-10(9.21±0.25)7	9-10(9.64±0.22)11	10-12(11.21±0.33)7	11-13(11.77±0.28)11	2(2.00±0)7	2(2.00±0)11
Honduras	9-10(9.33±0.54)3	9-11(9.92±0.30)13	10-12(11.00±0.94)3	10-13(11.92±0.28)13	1-2(1.60±0.68)3	1-2(1.92±0.11)13
Nicaragua	9(9.00±0)3	9-10(9.75±0.39)4	11-12(11.50±0.57)3	12-13(12.25±0.39)4	1-2(1.83±0.27)3	2(2.00±0)4
Costa Rica	9-10(9.22±0.10)38	8-11(9.56±0.01)57	10-12(11.04±0.16)38	10-13(11.76±0.12)57	1-3(1.89±0.08)37	2-3(2.04±0.04)57
Western Panama	9-10(9.17±0.43)3	9-10(9.46±0.31)7	10-11(10.33±0.54)3	10-12(10.86±0.50)7	2(2.00±0)3	2(2.00±0)7
(Northern Population)	9-10(9.20±0.08)54	8-11(9.64±0.09)94	10-12(11.05±0.14)54	10-13(11.75±0.10)94	1-3(1.90±0.07)53	1-3(2.02±0.03)94
(Osa Population)	8-10(9.00±0.66)3	9-11(10.00±0.45)4	10-12(10.67±0.86)3	11-13(12.00±0.45)4	2(2.00±0)3	2-3(2.25±0.48)4
Central Panamá	9-10(9.13±0.30)4	8-10(9.57±0.21)15	10-13(11.38±0.89)4	10-12(11.60±0.21)15	1-3(2.00±0.45)4	1-2(1.97±0.07)15
Colombia	8-11(9.15±0.12)27	9-10(9.52±0.13)30	10-12(10.65±0.16)27	10-13(11.73±0.18)30	1-3(1.94±0.13)27	1-4(2.20±0.13)30
Ecuador	9-10(9.10±0.23)5	9-10(9.25±0.39)4	9-11(10.30±0.48)5	11-12(11.63±0.43)4	2(2.00±0)5	2-3(2.38±0.43)4
(Southern Population)	8-11(9.14±0.10)36	8-10(9.51±0.10)49	9-13(10.68±0.17)36	10-13(11.68±0.13)49	1-3(1.96±0.11)36	1-4(2.14±0.09)49
Totals	8-11(9.18±0.06)93	8-11(9.60±0.07)147	9-13(10.89±0.11)93	10-13(11.73±0.08)147	1-3(1.92±0.06)92	1-4(2.06±0.04)147

oculabials are more than two is greater in Colombian and Ecuadorian specimens (21.2%) than in the remainder of the range (4.1%).

Supralabials and Infralabials. - The numbers of supralabials and infralabials average more in females than in males over the entire range (Table 5). All but one specimen (UMMZ 91078) have the first infralabials in contact.

Ventrals. - The number of ventral scales is slightly, but significantly higher in females than in males (Table 2) considering the range as a whole. A relatively high number of ventral scales is present in specimens of *B. nasuta* from western Panamá northward to México (129-145, $\bar{x} = 137.68 \pm 0.42$). A relatively low number exists in specimens from central Panamá southward to Ecuador (123-143, $\bar{x} = 132.15 \pm 2.58$).

Subcaudals. - As is usual in snakes, the subcaudals are more numerous in males than in females (Table 2), correlating with their greater relative tail length (Table 7).

Dorsal Scale Rows. - The dorsal scale rows usually number 25-23-19 (see description). Specimens from the Península de Osa are unusual, however, in possessing atypically high dorsal scale row counts (Table 6). Only one of the seven specimens available from there has the above-mentioned count. Two specimens have 25-25-19 rows, three have 27-25-19 rows, and a sixth has 29-27-19 rows. The latter specimen has the highest neck and midbody counts of any specimen examined.

Canthals. - All of the specimens that possess more than one canthal are from central Panama. Of 19 specimens from this area, 7 have two canthals on at least one side of the head; three specimens have two on both sides of the head.

Postcanthals. - Females show a higher incidence of two postcanthals (instead of one) than do males throughout the range (Table 4), with the exception of the sample from central Panamá. Viewed over the entire range, the differences are significant.

Color and Pattern. - Various aspects of color and pattern in *B. nasuta* vary individually, ontogenetically, sexually, and geographically.

There is considerable intrapopulational variation with some individuals being brightly marked on the head and body, whereas others are almost unicolor (see description).

The only series of specimens from a single locality from which adequate notes on ontogenetic color variation could be taken consists of twenty specimens from the Río Patia in southern Colombia (AMNH 107912-13, 109794-811). The juvenile specimens are noticeably brighter in color and more distinct in pattern than are the adults. In larger specimens the brownish gray ground color is basically the same but the brownish black to black dorsal blotches are faded and the whitish border of these blotches is indistinct. The fading of the pattern begins on the lateral portion of the dorsum and proceeds dorsad. The vertebral pale line is bright in the young and gradually fades in larger specimens, particularly females, until, in some specimens the line disappears altogether. In juveniles the dorsal blotches are discrete and well-defined, except for the first two or three blotches, which are reduced to small spots. As the animals increase in size, the blotches gradually fragment into two portions, which are laterally displaced from the middorsal line. This fragmentation and lateral displacement of the dorsal blotches proceeds from anterior to posterior.

Males generally possess a more contrasting facial and dorsal coloration than do females, although occasional dark male specimens are also seen. Males average more body blotches than do females and the values for the entire sample are significantly different (Table 1).

A living specimen from Ecuador in the senior author's private collection exhibits a peculiar temporary coloration prior to ecdysis. The animal is grayish

Table 6. Variation in dorsal scale rows in Bothrops nasuta (explanations as for Table 2).

	Males	Females
México	-	25(25.00±0)2
	-	23(23.00±0)2
	-	19(19.00±0)2
Guatemala	25(25.00±0)7	25-27(25.19±0.41)11
	23(23.00±0)7	23(23.00±0)11
	19-20(19.15±0.35)7	19(19.00±0)11
Honduras	25(25.00±0)2	25-27(25.36±0.49)12
	23(23.00±0)2	23-25(23.18±0.37)12
	19(19.00±0)2	19(19.00±0)12
Nicaragua	25(25.00±0)3	25(25.00±0)4
	23(23.00±0)3	23(23.00±0)4
	19(19.00±0)3	19(19.00±0)4
Costa Rica	23-27(24.92±0.52)39	23-27(25.08±0.14)57
	21-23(22.81±0.20)39	21-25(22.99±0.11)57
	19-20(19.03±0.32)39	17-21(19.01±0.10)57
Western Panamá	25(25.00±0)3	23-25(24.69±0.86)6
	23(23.00±0)3	23(23.00±0)7
	19(19.00±0)3	19(19.00±0)7
(Northern Population)	23-27(24.93±0.18)54	23-27(25.09±0.12)92
	21-23(22.85±0.14)54	21-25(23.02±0.08)93
	19-20(19.04±0.05)54	17-21(19.00±0.06)93
(Osa Population)	25-27(25.70±2.87)3	25-29(27.07±2.60)4
	23-25(24.37±2.87)3	25-27(25.53±1.60)4
	19(19.00±0)3	19(19.00±0)4
Central Panamá	23-25(24.53±1.60)4	23-25(24.75±0.39)15
	22-23(22.68±1.43)3	23(23.00±0)15
	19(19.00±0)4	19(19.00±0)15
Colombia	25(25.00±0)27	23-27(25.44±0.36)30
	23(23.00±0)27	23-25(23.22±0.11)30
	19(19.00±0)27	19-21(19.12±0.56)30
Ecuador	23-25(24.63±1.11)5	25-27(25.53±1.59)4
	21-23(22.63±1.11)5	23(23.00±0)4
	19(19.00±0)5	19-20(19.26±0.80)4
(Southern Population)	23-25(24.89±0.02)36	23-27(25.20±0.27)49
	21-23(22.91±0.13)35	23-25(23.13±0.14)49
	19(19.00±0)36	19-21(19.09±0.13)49
Totals	**23-27(24.94±0.13)93**	23-29(25.18±0.13)145
	21-25(22.92±0.12)92	21-27(23.12±0.10)146
	19-20(19.02±0.13)93	17-21(19.03±0.06)146

brown dorsally and powder gray ventrally. During the premolt period the ventrals and the first dorsal scale row and the ventral half of the second row turn a bright silver, contrasting markedly with the color of the remainder of the dorsum (Fig. 3).

Size and Proportions. - The average dimensions in head length, head width, head height, total length, and body length are greater in females than in males (Table 7; Fig. 4). Males possess a greater average relative tail length (Table 7), correlated with the higher average number of subcaudals (Table 2). Female specimens appear to be stouter than do males, but this feature is difficult to quantify because of variation caused by preservation.

Sex Ratios. - We sexed 240 specimens of *Bothrops nasuta*. A prevalence of females is present in collections from México southward through central Panamá (64.9% females vs. 35.1% males). The sex ratios in samples from Colombia and Ecuador are more evenly balanced (51.5% females vs. 48.5% males) (Table 1). Considering the number of specimens involved, it seems unlikely that these differences result simply from artifacts of collecting. The reasons for the greater percentage of females in samples from Panamá northward, however, remain obscure.

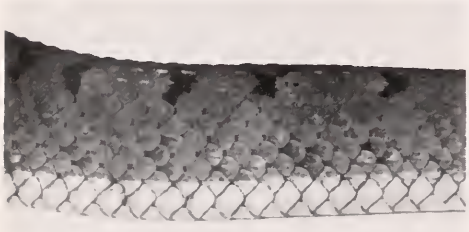

Figure 3. Section of body of a female *Bothrops nasuta* from Ecuador illustrating the marked contrast between the lower ventral color and that of the dorsum that is exhibited prior to ecdysis.

Figure 4. Adult male (lower) and female (upper) *Bothrops nasuta* from northern Honduras illustrating sexual dimorphism in size and the typical color pattern of members of the northern population.

DISCUSSION

On the basis of the foregoing analysis, the following characteristics have been shown to exhibit geographic variation in *Bothrops nasuta*: internasals; nasofrontals; intercanthals; interoculars; oculabials; ventrals; dorsal scale rows; canthals; color and pattern; sex ratios.

These characteristics show differing patterns of variation. The frequency of mutual internasal contact decreases markedly between samples from western and central Panamá. Ventral numbers are highest in the northern section of the range (western Panamá northward) and lowest in the southern section (central Panamá southward). Average numbers of interoculars are not significantly different between the sexes in samples from western Panamá northward, whereas the differenes are significant from that point southward. Central Panamanian specimens are distinctive in having a higher average number of nasofrontals, as well as being the only specimens possessing more than one canthal scale. Panamanian specimens have a higher average number of intercanthals than do specimens from the rest of the range. The preponderance of female specimens from the northern portion of the range south to and including central Panamá is

Table 7. Sexually dimorphic characters of size and proportions in *Bothrops nasuta* (measurements in millimeters - parenthetical numbers indicate range, mean, and sample size).

	Males	Females
Head length	11-24(17.0)93	12-37(22.6)147
Head width	7-15(11.3)93	8-28(14.9)147
Head height	4-10(6.6)93	4.14(8.6)147
Total length	162-463(291.1)88	156-635(349.0)139
Tail length	20-62(36.2)88	16-64(35.7)139
Body length	142-401(254.9)92	140-571(313.4)142
Tail/total length ratio	0.103-0.137(0.124)88	0.092-0.122(0.103)139

in marked contrast to the more even sex ratio in samples from Colombia and Ecuador. Specimens from Colombia and Ecuador have higher average numbers of oculabials than do specimens from the remainder of the range. The Península de Osa specimens are distinctive due to: (1) a higher number of dorsal scale rows on the neck and at midbody; (2) the juvenile tail color persisting into adulthood; (3) the shape and degree of elevation of the internasal scales, and (4) a distinctive dorsal body coloration.

Obviously, the most distinctive specimens are those occurring in the Península de Osa. Due to the small number of specimens available from this area, however, it remains an area in need of critical study. Other, less distinctive geographical groupings may be circumscribed as well. The patterns of variation in the samples of populations of *B. nasuta* outside of the Península de Osa are such that no clear cut distinctions can be drawn (i.e., the patterns of variation are discordant). On the other hand, the pattern of variation in several characters (frequency of mutual internasal contact; number of ventrals; nasofrontals, canthals, and intercanthals; sexual differences in average numbers of interoculars; and sex ratios) is such that a number of changes in those patterns occur in Panamá, with the most obvious changes occuring between western and central Panamá. Specimens from central Panamá, therefore, in general resemble specimens from South America, whereas those from western Panamá resemble specimens to the north (excluding those from the Osa Peninsula).

On the above basis, therefore, we prefer to recognize three distinctive populations of the hognose viper, *Bothrops nasuta*: the northern, Osa, and southern populations. Inasmuch as these populations do not exhibit equivalent levels of divergence, we do not recognize infraspecific taxa. We feel that to do so would tend to obscure the complex relationships we have detailed above. The populations are characterized below.

The Northern Population. - This population extends from southern México southward to the Boca de Almirante area of western Panamá, with the exception of the Península de Osa-Golfito area of southern Costa Rica. This population is characterized by having a greater incidence in the mutual contact of the internasal scales (98.6% of the specimens examined), a higher average number of ventral scales (males, 129-143, $\bar{x}$=136.98; females, 128-145, $\bar{x}$=138.14), a lower average number of nasofrontal scales (males, 22-46, $\bar{x}$=33.77; females, 25-54, $\bar{x}$=35.78), and a lower mean number of oculabials (96.6% of specimens having two or fewer). Typical examples from this population are illustrated in Figure 4.

The Osa Population. - This population is confined to the Península de Osa-Golfito area of southern Costa Rica and possibly adjacent western Panamá. This population is characterized by having a higher mean number of dorsal scale rows at the neck and midbody, the tendency of juvenile tail color to persist into adulthood (especially on the underside of the tail), a lesser degree of eleva-

tion of the anterior portion of the internasal scales, and a tendency for possession of transverse body bands (Fig. 5), as opposed to alternating blotches or spots.

The Southern Population. - This population occurs from Valle de Antón and the Canal Zone in central Panamá southward to Ecuador. This population is characterized by having a relatively low incidence of mutual contact of the internasal scales (52.4% of specimens examined), a lower average number of ventral scales (males, 123-141, $\bar{x}$=130.57; females, 127-143, $\bar{x}$=133.35), a higher average number of nasofrontal scales (males, 25-56, $\bar{x}$=40.14; females, 29-59, $\bar{x}$=42.84), and a higher mean number of oculabials (17.6% of specimens having three or more).

Biogeographic History. - Recently several authors have shown that alternating dry and humid climatic periods and sea level fluctuations occurring during the Pleistocene have had a marked effect on the evolution and distribution of Neotropical vertebrates (van der Hammen, 1961; Haffer, 1969; Vuilleumier, 1971; Duellman, 1979). In addition, several recent taxonomic studies on South American and Central American amphibians and reptiles have shown a close correlation between evolutionary events in the group in question and the paleogeographic events detailed in the above-cited papers (Vanzolini and Williams, 70; Duellmn, 1972; Heyer, 1973; Duellmn and Crump, 1974; Wilson and Mena 1980).

Figure 5. Adult female *Bothrops nasuta* (USCCRE 6391) from Rincón de Osa, Puntarenas Province, Costa Rica, illustrating the dorsal pattern of transverse bands.

Although the evolutionary relationships of the *Bothrops lansbergi* group, to which *B. nasuta* belongs, are imperfectly known, Burger (1971) expressed the opinion that the members of the *lansbergi* group, as well as those of the *godmani* and *nummifera* groups constitute a distinct genus, *Porthidium*. He stated that

"the *lansbergi* and *nummifera* groups diverged independently from the *godmani* group." In addition, he opined that "*Porthidium nasutum*, which is similar to *P. godmani* in some respects and specialized in others, is close to the ancestry of the *lansbergi* group." For these reasons we assume, for the present, that the point of origin of the species *B. nasuta* lies somewhere in Nuclear Central America and, most likely, southern México.

On the basis of information in the above-cited papers, we postulate the following sequence of events to account for the evolutionary history of *Bothrops nasuta*:

1. Movement of the *B. nasuta* stock from the north (probably southern México) into Central America during the upper Pliocene along the eastern humid corridor.
2. Movement of the stock of the Osa population into southern Pacific Costa Rica through low plateaus and/or narrow river canyons in the uplifting Talamanca range during the turn of the Pliocene-Pleistocene.
3. Isolation of the Osa population in the Península de Osa by rising sea levels during the interglacial periods of the Pleistocene.

4. Isolation of the northern and southern populations in wet forest refugia in Caribbean Central America and the Pacific side of Colombia, respectively, during a period of dry forest expansion in the Quaternary.

SPECIMENS EXAMINED

Locality data for each specimen examined are listed below. The data are arranged as follows: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museums, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed in the first most restricted political unit possible. Localities enclosed by quotation marks are not mapped.

The localities and specimens are: COLOMBIA: "Boca de la Raspadura," AMNH 18298-300. *Antioquia*: "Medellín," AMNH 35735; Río Arquía, Belen, LACM 45413; Sabanalarga, Cauca Valley, AMNH 35795. *Cauca*: Quebrada Guanguí, 0.5 km above Río Patía, 100-200 m, AMNH 109794-811; Quebrada Guanguí, Río Patía, 100 m, AMNH 107912-13. *Chocó*: "no specific locality," AMNH 8067-68; Andagoya, MCZ 29255, USNM 124259, Andagoya-Condota area, UMNZ 121043-44; between Andagoya and Condota, UMMZ 121058; vic. Playa de Oro, upper Río San Juan, 200 m, AMNH 108460; Quebrada Taparal, 20 km N Palestina, CAS 119919; Río Atrato, S of Quibdó, USNM 140050; Río San Juan, USNM, 72352; Sierra de Baudó, ANSP 25573-78; trail between Quebrada Bochoramá and Río Tadocito, LACM 45416. *Valle*: Buenaventura, at Rockerfeller Lab, 12 m, TU 18712; km 13 from Buenaventura to Río Calima, 45 m, FMNH 165478, 165893; near Buenaventura on land of Cartón de Colón, TU 18711; Río Calima, Quebrada de la Brea, USNM 124260; Río Calima, 7 km from lumber camp, FMNH 165492, 165495, 165566, 165725-26, 165900; Rio Paposo, Virology Field Station, USNM 151711-12.

"COLOMBIA or ECUADOR": USNM 22422.

COSTA RICA: "Hospital San Juan de Dios," KU 34636; "Costa Rica,"UF 20627, 30709, UMMZ 133893, 133911. *Alajuela*: Cantón de San Carlos, Muelle San Carlos, 65 m, USC-CRE 2711; Cariblanco, UCR 1431; Cataratas de San Ramon, Lado San Carlos, USC-CRE 2754; Ciudad Quesada, 656 m, USC-CRE 2693; Ciudad Quesada, San Roque, 580 m, USC-CRE 2695; San Carlos, FMNH 191789, UMMZ 131327-29; Sarapiquí, 100m, UCR 109, 2990, USC-CRE 2691. *Cartago*: Pavones, nr. Turrialba, 819 m, KU 140087, LSUMZ 36898-99, USC-CRE 2710; Turrialba, 624 m, KU 30982-87, 34876, 34879-80, 35734-35, MCZ 55067-74, UCR 1870; Turrialba, IICA, 600-624 m, AMNH 69722, FMNH 179083, KU 25689, 34635, 34637-38, MCZ 56116, USC-CRE 646; Turrialba, 3 km from IICA on road to Pavones, 630 m, USC-CRE 190. *Guanacaste*: El Silencio de Tilarán, 825-850 m, USC-CRE 6217; 5 km ENE Tilarán, 600 m, KU 36693; Tilaran, 560-562 m, KU 35737-38, USC-CRE 2694, 2712, 7131, 7163. *Heredia*: "no specific locality," UF 30492, 30495, 30498, 31795-96; La Selva, central trail, 60 m, USC-CRE 8291. *Limon*: La Lola, 39 m, KU 34005, UMMZ 117736-37, USC-CRE 127 (2 spec.), 128 (3 spec.), 140 (2 spec.), 162, 203, 207, 655 (2 spec.); Limón, MCZ 19744; Los Diamantes, UMMZ 117738; nr. Penshurst, HSH/RSS 600; Penshurst, UCR 2721-22, 2738-39, 2940-41; Puerto Viejo, UCR 162; 4 km E Puerto Viejo, UCR 308; Suretka, nr. Mt. Mirador, KU 35736; Sipurio, Talamanca, AMNH 17332; Zent, MCZ 11457-58. *Puntarenas*: "no specific locality." UMMZ 83185; Golfito, 5 m, USC-CRE 836; 6.7 km E Golfito, LSUMZ 11652; Rincón de Osa, LACM 114153-54; vicinity of Rincon de Osa, 20-40 m, USC-CRE 6391; Rincon de Osa, Camino del Pacifico, UCR 3310, 3359. *San José*: Puriscal, UCR 110.

ECUADOR: *Esmeraldas*: Playa de Oro, Santiago River, USNM 20625-28; Quinindé, USNM 165317; Río Capapas, MCZ 11169. *Pichincha*: 18 km W Santo Domingo de los Colorados on Chono road, USNM 165320; 5 km W Santo Domingos de los Colorados, USNM 165321; 12 km NW Santo Domingo de los Colorados on Quinindé Road, USNM 165319. USNM 165319.

GUATEMALA: *Alta Verapaz*: Finca Chamá, UMMZ 91077-78. *El Petén*: 12 km NW Chinajá, 130 m, KU 55705; Piedras Negras, USNM 110415; Sayaxché, UCM 22367; Sojío (=Toocog), AMNH 69966-67, 69987; Tikal, 283 m, MCZ 55436-37, UF 13866, 13868-69, UMMZ 117944; 4.8 km S Tikal, KU 157665; 13.5 mi S Tikal, KU 157664; Valontun, 4 km SE Tikal, AMNH 100410. *Izabal*: 12.8 km SE Cayo Piedra, 153 m, ANSP 22149.

HONDURAS: *Atlántida:* Dakota, East Line, MCZ 20247; Jilamo, MCZ 34385; Lancetilla, AMNH 46958-60, MCZ 38781; Sonora Farm, Taujica District, MCZ 20493; Tela, AMNH 46961; Tela, Juliana Farm, MCZ 22023. *Cortés:* La Cumbre, nr. San Pedro Sula, MCZ 32028; San Pedro Sula, MCZ 33332-33. *Snata Barbara:* Santa Barbara, MCZ 27566; Trinidad, MCZ 27565. *Yoro:* Progreso, MCZ 22024, 26872-UMMZ 62522.

MÉXICO: *Chiapas:* Lake Miramar, USNM 136966-67. "Veracruz," ANSP 4873.

NICARAGUA: "vicinity of Poderoso," AMNH 12706. *Matagalpa:* "no specific locality," UMMZ 57654; Hacienda La Cumplida,

900m, UMMZ 117735; 19 km N Matagalpa, UMMZ 116523. *Río San Juan*: Los Sabalos, San Juan River, AMNH 28355. *Zelaya*: Eden Mine, AMNH 7411; Río Huahuashán, Papel Camp, AMNH 70247.

PANAMÁ: "Panama City," MCZ 37115-16. *Bocas del Toro*: Almirante, FMNH 83466, 153847, KU 80247, 112597; 11 km NW Almirante, FMNH 153849, 153851-52, 153999; 12 km NW Almirante, UU 5564. *Canal Zone*: Chico Limpio Divide, 470 m, MCZ 42767; Madden Dam, ANSP 23889; nr. Miramar River, 183 m, MCZ 42768; Pequeni-Esperanza Ridge, 214-610 m, MCZ 42772-81. *Coclé*: El Valle de Antón, 550 m, KU 112596; El Valle de Antón, Finca Acre, FMNH 68054-56. *Panamá*: nr. Boquerón, Candelaria, and Peluca Station, AMNH 68850.

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BELIZE: Xuanantunich (Neill, 1965).

COLOMBIA: *Antioquia*: Segovia (Nicéforo María, 1942); "Urrao" (Nicéforo María, 1938, 1942); Zea District (Posada-Arango, 1889). *Caldas*: "Pueblo Rico" (Nicéforo María, 1938, 1942). *Chocó*: Cabeceras (Rendahl and Vestergren, 1941); Quibdó (Nicéforo María, 1942.

GUATEMALA: *Alta Verapaz*: Panzos (Bocourt, 1868).

MEXICO: *Chiapas*: Rancho Alejandría, Municipio de Juárez (Alvarez del Toro, 1973).

NICARAGUA: "Hacienda de Jericho [=Jerico], 991 m" (Gunther, 1895; Boulenger 1896); "Chontales" (Günther, 1895; Boulenger, 1896). *Río San Juan*: Greytown (Amaral, 1929a).

PANAMÁ: *Canal Zone*: "Cerro Bruja" (Amaral, 1929a; Schmidt, 1933; Dunn and Bailey, 1939).

ACKNOWLEDGMENTS

We would like to thank the following people for allowing us to examine material in their care: Walter Auffenberg, Florida State Museum, University of Florida (UF); William E. Duellman and Julian C. Lee, Museum of Natural History, University of Kansas (KU); Harold A. Dundee, Tulane University (TU); Herbert S. Harris and Robert S. Simmons, Natural History Society of Maryland (HSH/RSS); Arnold G. Kluge, University of Michigan, Museum of Zoology (UMMZ); John M. Legler and Robert M. Winolur, Museum of Zoology, University of Utah (UU); Alan E. Leviton, California Academy of Sciences (CAS); Hymen Marx, Field Museum of Natural History (FMNH); T. Paul Maslin, University of Colorado Museum (UCM); Edmond V. Malnate, Academy of Natural Sciences, Philadelphia (ANSP); Douglas C. Robinson, Universidad de Costa Rica (UCR); Douglas A. Rossman, Museum of Zoology, Louisiana State University (LSUMZ); Jay M. Savage, University of Southern California-Costa Rica Expedition (USC-CRE); Ernest E. Williams, Museum of Comparative Zoology (MCZ); John W. Wright, Los Angeles County Museum of Natural History (LACM); George R. Zug, National Museum of Natural History (USNM); Richard G. Zweifel, American Museum of Natural History (AMNH).

We would also like to thank Jay M. Savage for providing us with information concerning a locality in Costa Rica, Roy W. McDiarmid and Charles W. Myers for providing us with photographs of *Bothrops nasuta*, and Albert Schwartz for bringing to our attention the matter of the correct spelling of the specific name for the species.

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SOME TREMATODES OF MAMMALS IN LOUISIANA

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ABSTRACT

The following trematodes were collected from mammals in southern Louisiana: Alaria mustelae Bosma, 1931 from the raccoon, *Procyon lotor* (Linn.); *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 from raccoons, opossums (*Didelphis virginiana* Kerr), and a mink, *Mustela vison* Schreber; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from a raccoon and a gray fox, *Urocyon cinereoargenteus* (Schreber); *Pharyngostomoides procyonis* Harkema, 1942 from the raccoon; *Heterobilharzia americana* Price, 1929 from raccoons and opossums; *Apophallus venustus* (Ransom, 1920) Cameron, 1936 from raccoons; *Parametorchis complexus* (Stiles and Hassal, 1894) Skrjabin, 1913 from raccoons; *Baschkirovitrema incrassatum* (Dies., 1850) Skrjabin, 1944 from an otter, *Lutra canadensis* (Schreber); *Brachylaima virginianum* Dickerson, 1930 from opossums; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961 from raccoons; *Hasstilesia texensis* Chandler, 1929 from swamp rabbits, *Sylvilagus aquaticus* (Bachman); *Maritreminoides nettae* (Gower, 1938) Rankin, 1939 from raccoons; and *Rhopalias macracanthus* Chandler, 1932 from opossums. *Brachylaima virginianum, Fibricola cratera, F. lucida, Hasstilesia texensis, Heterobilharzia americana,* and *Rhopalias macracanthus* have been previously reported from Louisiana; the other species are new locality records. The raccoon is a new host record for adult *Alaria mustelae*. Diagnoses are presented for species representing state records along with pertinent notes on the epidemiology and zoogeography of each.

INTRODUCTION

During our studies on the life cycle of *Alaria marcianae* (La Rue, 1917) Walton, 1949 in Louisiana we had the opportunity to examine other mammals for trematodes. All mammals reported herein were collected in southern Louisiana from an area bordered on the west by the Atchafalaya basin and on the east by Lake Maurepas. The mammals were collected by leg traps set in and around cypress-tupelo swamps.

The following mammals were examined for trematodes, one mink, *Mustela vison* Schreber; one gray fox, *Urocyon cinereoargenteus* (Schreber); one striped skunk, *Mephitis mephitis* (Schreber); two river otters, *Lutra canadensis* (Schreber); two swamp rabbits, *Sylvilagus aquaticus* (Bachman); twelve opossums, *Didelphis virginiana* Kerr; and thirty raccoons, *Procyon lotor* (Linn.).

Trematodes were fixed in steaming 10% formalin and stained in Semichon's aceto-carmine. All measurements are in micrometers unless otherwise stated; means are followed by the ranges in parentheses. Line drawings were prepared with the aid of a microprojector. Representative specimens for which diagnoses are given were deposited in the Manter Laboratory, University of Nebraska State Museum.

The following is a list of trematodes we found from mammals that have been previously reported from Louisiana: From the mink we found *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 in the small intestine; both swamp rabbits harbored thousands of *Hasstilesia texensis* Chandler, 1929 in the small intestine; in opossums *F. cratera* and *Rhopalias macracanthus* Chandler, 1932 occurred in the small intestine of all twelve, *Brachylaima virginianum* Dick-

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erson, 1930 in the small intestine of eight, and *Heterobilharzia americana* Price, 1929 in the mesenteric venules of three; from gray fox we have a single specimen of *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from the small intestine; no trematodes were found in the skunk; and in the raccoons we collected *F. cratera* and *F. lucida* from the small intestine of ten and one respectively, and *H. americana* in the mesenteric venules of four.

Lumsden and Zischke (1961) adequately described *Fibricola cratera, F. lucida, Hasstilesia texensis,* and *Brachylaima virginianum* from Louisiana mammals. Malek et al. (1961) studied *Heterobilharzia americana* in southern Louisiana and found the raccoon to be the principal definitive host. Kaplan (1964) was the first to report *H. americana* from the opossum and commented on its rarity in marsupials. In addition to these previously reported trematodes we have identified seven species, one from the otters and six from the raccoons, that have not been reported from Louisiana and are of importance from either epidemiological or zoogeographical standpoints.

Family DIPLOSTOMIDAE Poirier, 1886

Alaria mustelae Bosma, 1931
(Figure 1)

Synonyms: *Alaria freundi* Sprehn, 1932; *A. intermedia* (Olivier and Odlaug, 1938) Odlaug, 1940; *A. dubia* Chandler and Rausch, 1946; *A. minuta* Chandler and Rausch, 1946, *A. taxidea* Swanson and Erickson, 1946; *A. canadensis* Webster and Wolfgang, 1956.

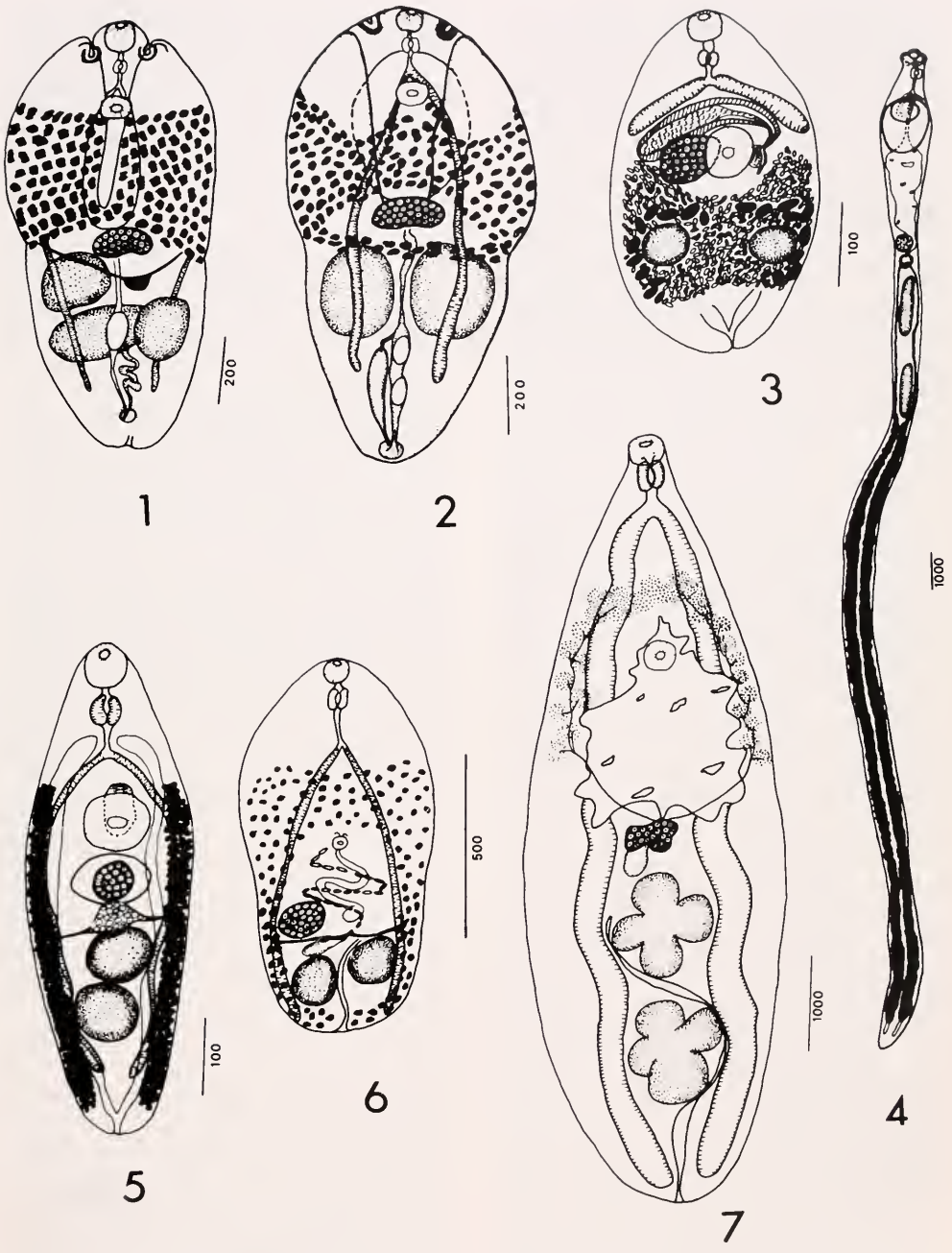
Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Bayou Duplantier (East Baton Rouge Par.); 2 mi. N. of Hwy. 190 on Atchafalaya River (Pointe Coupee Par.). Univ. Nebraska State Mus., Manter Lab. Coll. No. 21194

Diagnosis (based on ten mature specimens): Body indistinctly bisegmented, 1250 (1160-1420) long; forebody scoop-shaped, 680 (650-770) long by 565 (500-580) wide, with pseudosuckers present on both sides of oral sucker; hindbody conical, 540 (460-650) long by 470 (450-530) wide, containing reproductive organs. Forebody cuticle completely covered with small spines; hindbody smooth. Oral sucker terminal, 86 (80-95) long by 81 (70-90) wide. Prepharynx present, short. Pharynx 66 (60-70) long by 48 (45-50) wide. Esophagus short, often not apparent. Ceca terminate near posterior end of body. Acetabulum wider than long, 73 (70-80) long by 90 (85-93) wide. Holdfast broadly oval, variable in size, anterior extension partially or completely covers the acetabulum. Testes two, not equal; anterior testis irregularly oval, laterally displaced on either side of midline, 188 (155-230) long by 206 (190-230) wide; posterior testis dumbbell-shaped, much wider than anterior testis, 183 (150-220) long by 335 (355-400 wide, posterior testis with ventro-medial groove to allow passage of ceca and uterus. Seminal vesicle expanded into a muscular ejaculatory duct. Ovary reniform, located at forebody-hindbody juncture, 94 (90-100) long by 147 (135-155) wide. Mehlis gland opposite anterior testis. Uterus makes an initial course into holdfast region and then passes posteriorly emptying into the genital atrium. Genital atrium posterior, subterminal on dorsal surface. Vitellaria occupies much of the forebody from the acetabulum to anterior testis, never observed posterior to anterior testis. Vitelline ducts unite to form a vitelline reservoir at the level of anterior testis. Eggs large, few, 106 (102-110) long by 63 (60-65) wide. Excretory pore subterminal on ventral side.

Discussion: Babero (1960) tentatively listed *Alaria taxidea* as an intestinal inhabitant of the skunk, *Mephitis mephitis*, in Louisiana. Johnson (1979) relegated



Figures 1-7. 1. *Alaria mustelae,* ventral view, from *Procyon lotor.*2. *Pharyngostomoides procyonis*, ventral view, from *Procyon lotor*. 3. *Maritreminoides nettae*, ventral view, from *Procyon lotor*. 4. *Baschkirovitrema incrassatum*, ventral view, from *Lutra canadensis*. 5. *Gyrosoma singulare*, ventral view from *Procyon lotor*. 6. *Apophallus venustus*, ventral view, from *Procyon lotor*. 7. *Parametorchis complexus,* ventral view, from *Procyon lotor*. Scale in micrometers.

A. taxidea to a junior synonym of *A. mustelae* based on life history and host specificity for mutelids. He demonstrated that specimens of *A. mustelae differed in size and morphology when recovered from different mustelid hosts. He found no natural A. mustelae* infection in the raccoons he examined, but 1000 mesocercariae fed to a single raccoon yielded 14 adults. They were similar morphologically to those from mustelid infections, but were decidedly smaller. Bosma (1934) stated that she recovered only *A. mustelae* metacercariae from raccoons.

This is the first report of natural infections of adult *Alaria mustelae* in raccoons. We found two of thirty raccoons infected. One infection consisted of fifteen worms whereas the second infection consisted of several hundred mature adults in the small intestine. Our specimens are smaller (1.160-1.420 mm) compared to the upper range (2.4 mm) of the species reported by Johnson (loc. cit.), but are larger than his specimens from the experimental infections in the raccoon (0.88-1.00 mm). Unfortunately Babero (loc. cit.) did not list measurements for his specimens from skunks and we were unsuccessful in gaining access to them. However, we concur that *A. taxidea* is a synonym of *A. mustelae* and that the low number of naturally infected raccoons, small size of worms, and the low number of adults recovered in experimental infections of raccoons indicates a physiological specificity for mustelids.

Of interest from an epidemiological standpoint, Beaver et al. (1977) reported a mesocercarial infection in a human in Louisiana. They believed the mesocercariae members of the genus *Alaria* and traced the infection to the consumption of an undercooked raccoon. Johnson (loc. cit.) has proven experimentally, and we have found in nature, that raccoons may serve as definitive hosts for *A. mustelae*. However, given the low specificity of *A. mustelae* for raccoons and the complex migration of all species of *Alaria* in the definitive host (gut to lungs and back to gut) some mesocercariae may lose their way and lodge in other tissues. We have evidence to this effect in other species of *Alaria* (to be presented elsewhere). This indicates that the raccoon is not only a definitive but a paratenic host as well.

Pharyngostomoides procyonis Harkema, 1942
(Figure 2)

Synonyms: *P. ovalis* Chandler and Rausch, 1946.

Hosts: *Procyon lotor* (Linn.)

Location: Small intestine.

Localities: St. Landry, Pointe Coupee, Iberville, St. Martin, East Baton Rouge, Ascension, and Livingston parishes.

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21195.

Diagnosis (based on ten mature specimens): Body indistinctly bisegmented, 1160 (1080-1250) long; forebody scoop-shaped, 580 (520-620) long by 570 (520-630) wide, with pseudosuckers present on both sides of the oral sucker; hindbody conical, 580 (540-620) long by 506 (450-550) wide. Forebody cuticle completely covered with small spines; hindbody smooth. Oral sucker terminal, 74 (70-75) long by 90 (80-95) wide. Prepharynx 10 (5-15) long. Pharynx muscular, 57 (50-60) long by 51 (45-55) wide. Esophagus 22 (20-25) long. Ceca extend just posterior to testes, never reaching posterior end of body. Acetabulum spherical, posterior to intestinal bifurcation, 77 (75-80) long by 78 (75-80) wide, artially or completely covered by holdfast organ. Holdfast well developed, elongate, broadly oval, may reach as far as pharynx. Testes equal, spherical or oval, opposite but often diagonal, 237 (200-250) long by 200 (180-230) wide, located in hindbody dorsal to ceca. Seminal vesicle coiled,posterior to testes, expanded into a muscular ejaculatory pouch, that terminates in a genital cone. Genital atrium posterior, subterminal on dorsal side. Ovary reniform or trans-

versely oval, anterior to testes, 90 (85-100) long by 137 (125-160) wide. Uterus makes a short ascending loop into holdfast region, turns posteriorly and unites with ejaculatory pouch. Vitellaria mainly in forebody, extending from acetabulum to the anterior margin of testes. Vitelline ducts unite just posterior to ovary to form the vitelline reservoir. Eggs few, large, 92 (90-95) long by 60 (58-62) wide. Excretory pore subterminal on ventral side.

Discussion: *Pharyngostomoides* is a stenoxenic genus reported only from raccoons. Harkema (1942) described *P. procyonis* from raccoons in North Carolina and Texas. *P. ovalis* was subsequently described by Chandler and Rausch (1946) in Michigan and was later synonymized with *P. procyonis* by Dubois (1963). Harkema and Miller (1964) surveyed raccoons from North Carolina, South Carolina, Georgia, Florida, and Virginia and found *P. procyonis* present in each state. Further, they noted that there appeared to be two forms present in the raccoon. Beckerdite et al. (1971) raised both of these forms to full species. They described *P. adenocephala* and separated it from *P. procyonis* on the basis of: 1) larger size; 2) *shape (spathulate rather than scoop*-shaped); 3) presence of pseudosucker glands; 4) absence of an ejaculatory pouch; and 5) morphology of larval stages.

Based on our dignosis we conclude that our specimens belong to *P. procyonis*. We are not able to compare the morphology of the larval stages since the life history in Louisiana is unknown. We have found *P. procyonis* to be the most frequent parasite encountered in raccoons; 29 of 30 examined were infected with this worm. The only exception was a raccoon collected near a residential area of Baton Rouge. Infections ranged up to an estimated 5000 worms in one raccoon.

Family MICROPHALLIDAE Travassos, 1920

Maritreminoides nettae (Gower, 1938) Rankin, 1939

(Figure 3)

Synonyms: *Maritrema nettae* Gower, 1938; *Pseudospelotrema nettae* (Gower, 1938) Hunter and Vernberg, 1953.

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Atchafalaya R. at Krotz Springs (St. Landry Par.); 5 mi. N. of Butte La Rose on Atchafalaya R. (St. Martin Par.); 10 mi. S. of Ramah on East Atchafalaya Protection Levee (Iberville Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21196

Diagnosis (based on ten mature specimens): Body small, pyriform, 407 (390-420) long by 231 (220-270) wide. Cuticle completely covered with small spines. Oral sucker subterminal, 45 (37-50) long by 57 (55-61) wide. Prepharynx 25 (15-33) long. Ceca short, thickwalled, bifurcating anterior to cirrus sac and extending toward edges of body; never extending past anterior level of acetabulum, 130 (120-143) long. Acetabulum pre-equatorial, larger than oral sucker, 63 (57-66) long by 63 (61-68) wide. Testes spherical, opposite, equal in size, 71 (60-83) long by 70 (60-77) wide. Cirrus sac crescent-shaped, transverse, preacetabular; walls of cirrus sac thick with well developed seminal vesicle, prostate, and ejaculatory duct; ejaculatory duct extends into a slender, protrusible cirrus. Genital atrium opens sinistral to acetabulum; atrium armed with small, stout spines. Ovary irregularly oval, usually overlapping acetabulum, 71 (64-81) long by 79 (75-80) wide. Uterus consists of loops between acetabulum and posterior stem of excretory vesicle. Vitellaria form a right angle to testes with the sides being anterior and lateral to each testis, a few follicles extend posterior to testes but never reach end of body. Eggs small,

numerous, 20 (20-22) long by 11 (10-11) wide. Excretory pore terminal; excretory vesicle V-shaped.

Discussion: Rankin (1939) erected the genus *Maritreminoides* for those microphallids with a long, protrusible cirrus and antero-lateral uterine coils. He placed in his genus *M. nettae* and two metacercarial forms from fishes; *M. obstipum* (Van Cleave and Mueller, 1932) and *M. medium* (Van Cleave and Mueller, 1932). Etges (1953) regarded the genus *Maritreminoides* valid, but transferred *M. obstipum* and *M. medium* into the genus *Maritrema* Nicoll, 1907 because they did not possess a protrusible cirrus. Sogandares-Bernal (1965) surveyed crayfishes in Louisiana for parasites and reported *Maritrema obstipum* from *Cambarellus shufeldti* (Faxon, 1881) and *Procambarus clarkii* (Girard, 1852). The metacercaria figured by Sogandares-Bernal is morphologically identical with the adult worms we have found in raccoons except for lacking a protrusible cirrus and being ovigerous. Presumably, Sogandares-Bernal assigned the metacercariae to the genus *Maritrema* based on the absence of a protrusible cirrus.

We believe the metacercariae found in crayfishes by Sogandares-Bernal (loc. cit.) to be the larval stage of the adults we have collected from raccoons. The fact that a cirrus was not figured for the metacercaria could well have been because the worms were immature. Functionally, a protruded cirrus in a metacercarial stage, unless progenetic, would be of dubious value. The location of the infected crayfishes, as reported by Sogandares- Bernal, is in the same basin as are the infected racoons. We have observed crayfish remains in many raccoons.

Though *Maritreminoides nettae* was described from ducks in Michigan (Gower, 1938), Harkema and Miller (1964) reported it from raccoons in North Carolina, South Carolina, and Georgia. We reported the finding of *M. nettae* in the small intestine of seven of thirty raccoons in Louisiana. We also report what we believe to be the second intermediate host, i.e. the crayfishes of Sogandares-Bernal (loc. cit.). If life histories of closely related forms are examined, the first intermediate host of *M. nettae* is most probably an amnicolid snail.

Family ECHINOSTOMATIDAE
(Looss, 1902) Poche, 1926.

Baschkirovitrema incrassatum (Diesing, 1850) Skrjabin, 1944
(Figure 4)

Synonyms: *Dipostomum incrassatum* (Diesing, 1850; *Echinostomum incrassatum* (Diesing, 1850) Stossich, 1891.

Hosts: *Lutra canadensis Schreber.*

Location: Small intestine.

Locality: Lake Verret (Assumption Par.)

Univ. Nebraska State Mus., Manter Lab., Coll. No. 21197.

Diagnosis (based on 14 mature specimens): Body elongate, slender, 27.5. (23-31) mm long. Maximum width at level of acetabulum, 1170 (1100-1300). Head color reniform, 546 (500-580) wide, bearing 27 spines; a double row of 4 corner spines on each side, 148 (140-160) long by 42 (35-50) wide; six lateral spines on each side are found in a single row and are increasingly larger from ventral to dorsal side, the largest lateral spine, 121 (100-145) long by 26 (25-30) wide; 7 dorsal, uninterrupted spines, 132 (120-150) long by 25 (24-26) wide. Oral sucker 262 (220-280) long by 287 (250-300) wide. Prepharynx 142 (130-150) long. Pharynx 240 (220-250) long by 170 (140-200) wide. Esophagus 690 (600-800) long. Ceca two, terminating near posterior end of body. Acetabulum very prominent, muscular, located in anterior fifth of body, 1190 (1100-1400) long by 990 (900-1050) wide. Testes tandem, elongate, oval, in anterior third of body; anterior testis 1190 (970-1450) long by 265 (200-320) wide; posterior testis 1090 (870-1400) long by 246 (200-310) wide.

Vas efferens originate on antero-lateral side of testes and unite at posterior margin of the acetabulum; cirrus sac dorsal, not extending posterior to the acetabulum, 1150 (1100-1400) long by 500 (400-550) wide; cirrus long, slender, and unarmed. Ovary round, dextral to midline, 300 (240-350) long by 260 (250-280) wide. Mehlis gland diffuse, immediately posterior to ovary. Uterus with short descending coil; ascending uterus forms transverse intercaecal loops between Mehlis gland and acetabulum; distal vessel of uterus forms a metraterm that opens at the common genital pore just anterior to acetabulum. Vitelline follicles extend from middle of anterior testis to posterior end of body, filling most of lateral space behind testes. Vitelline ducts originate at middle of anterior testis and unite to form a vitelline reservoir at level of Mehlis gland. Excretory pore terminal. Eggs abundant, 109 (105-115) long by 64 (60-66) wide.

Discussion: The geographical localities from which *Baschkirovitrema incrassatum* have been reported are of considerable interest. Braun (1901) described *B. incrassatum* from the otter, *Pteronura brasiliensis* Zimmerman, in South America; Beverly-Burton (1960) and Myers et al. (1960) report *B. incrassatum* from *L. maculicollis* Lichtenstein and *Aonyx capensis* (Schinz) from Africa; and Sawyer (1961), Harkema and Miller (1968), and Fleming et al. (1977) have identified *B. incrassatum* from *L. canadensis* in North America.

Harkema and Miller (loc. cit.) reported *B. incrassatum* from North Carolina and stated that they compared their specimens with those of Sawyer (loc. cit.) from Georgia and to specimens deposited in the National Museum by W. J. Hamilton from otters in New York. They reported all specimens from North America were similar and that they "compared favorably" with the measurements given by Beverly-Burton (loc. cit.) from Africa. The present report is the first to present measurements from North American material. We have found that our specimens from Louisiana are much larger than those reported from South America (Braun, 1901) and from Africa (Beverly-Burton, 1960) and with no apparent overlap (Table 1). In addition, the oral sucker and acetabulum of our specimens are proportionately larger than previously described.

As indicated by the measurements, our specimens are more closely aligned with the material from South America than those from Africa. Since life histories of any of these forms are enigmatic, it is difficult to ascribe differences at this time to intra- or interspecific variation.

Family PSILOSTOMIDAE Looss, 1900

Gyrosoma singulare Byrd, Bogitsh, and Maples, 1961

(Figure 5)

Synonyms: Originally described as *Grysoma singularis* Byrd et al., but Yamaguti (1971) emended the genus to *Gyrosoma.*

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Localities: Bayou Duplantier and Spanish Lake (East Baton Rouge Par.); Atchafalaya R. between Keith Lake and Krotz Springs (St. Landry Par.); and Head of Island (Livingston Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No. 21198.

Diagnosis (based on ten mature specimens): Body lanceolate, relatively thick, 632 (580-680) long; widest at level of acetabulum, 222 (200-265) wide. Cuticle thick, beset with short, stout spines; spines set in dense rows anteriorly and become less numerous behind the posterior testis. Oral sucker subterminal, 55 (52-59) long by 56 (52-59) wide. Prepharynx 15 (13-17) long. Pharynx barrel-shaped, 35 (30-41) long by 36 (33-39) wide. Esophagus distinct, 14 (22-41) long. Ceca bifurcating anterior to common genital pore, diverge laterally to acetabulum and terminate midway between posterior testis and caudal end of body. Acetabulum prominent, pre-

Table 1. Comparative measurements of *Baschkirovitrema incrassatum* from Africa, South America, and North America.

	Africa Beverley-Burton (1960)	South America Braun (1901)	North America (present study)
Body length	12.50-16.55 mm	7-19 mm	27.5 (23-31) mm
No. of head spines	27	27	27
Corner spines	108-154 X 28-37	104 X 31	148 (140-160) X 42 (35-50)
Lateral spines	105-130 X 28-32	–	121 100-145) X 26 (25-30)
Dorsal spines	109-144 X 30-34	83-93 X 21	132 (120-150) X 25 (24-26)
Oral sucker: length	190-220	166-250	262 (220-280)
Oral sucker: diameter	220-260	187-208	287 (250-300)
Acetabulum: length	870-1170	–	1190 (1100-1400)
Acetabulum: diameter	810-950	1000	990 (900-1050)
Pharynx: diameter	120-210	73-83	170 (140-200)
Testes: length	1120-1500	1000	1140 (870-1450)
Testes: diameter	320-480	400	256 (200-320)
Ovary: length	320-390	330	300 (240-350)
Ovary: diameter	320-370	266	260 (250-280)
Eggs	108-123 X 54-62	104 X 73	109 (105-115) X 64 (60-66)

equatorial, 89 (81-92) long by 82 (70-92) wide. Testes oval, diagonal (rarely tandem), contiguous and often overlapping; anterior testis 76 (66-88) long by 85 (81-96) wide; posterior testis 86 (72-96) long by 83 (77-94) wide. Cirrus sac prominent, dorsal to acetabulum, containing seminal vesicle, well developed prostate, and a short, muscular cirrus. Genital pore midventral between cecal bifurcation and acetabvulum; a well developed sphincter muscle is observed when the genital pore is constricted. Ovary ovoid, lying immediately postero-dorsal to acetabulum, 45 (42-48) long by 42 (40-44) wide. Uterus short, ascends directly to genital pore; usually only one egg observed in the uterus at one time, but occasionally two. Egg thick-shelled, large in comparison with body size, 105 (100-110) long by 64 (60-75) wide. Vitellaria extend laterally from the genital pore to caudal end of body; each follicle composed of large, clearly defined vitelline cells. Vitelline ducts extend medially between testes and acetabulum to form a large vitelline reservoir. Excretory system composed of a terminal excretory pore; a Y-shaped excretory vesicle that bifurcates at caudal end of ceca; and arms that extend anteriorly to level of the pharynx.

Discussion: The genus *Gyrosoma* was created by Byrd et al. (1961) to accommodate specimens collected from a single raccoon in Georgia. They considered these worms to be distinct from other psilostomids based on: 1) the diagonal arrangement of the testes; 2) triangular shape of the testes; 3) a short uterus; and 4) a single, large egg in the uterus. To our knowledge, the only other mention in the literature of *G. singulare* is that of Harkema and Miller (1964) who state that they have also found it in Georgia and South Carolina.

We have collected *G. singulare* from the small intestine of 24 raccoons in Louisiana. Infection ranged from a few to several hundred worms. This appar-

ently stenoxenic species is most easily distinguished by the presence of a large egg which may approach one fourth the size of the worm. No morphological data have been reported for this species other than that contained in the original description. Our measurements significantly extend the size range of this species (580-680 compared to 290-480) and we find that our specimens have more spherical shaped testes than the triangular or half-mooned shape reported by Byrd et al. (loc. cit.).

Family HETEROPHYIDAE (Leiper, 1909) Odhner, 1914

Apophallus venustus (Ransom, 1920) Cameron, 1936
(Figure 6)

Synonyms: *Cotylophallus venustus* Ransom, 1920; *C. similis* Ransom, 1920; *Rossicotrema venustum* Ciurea, 1924.

Hosts: *Procyon lotor* (Linn.).

Location: Small intestine.

Locality: 10 mi. S of Ramah on the East Atchafalaya Protection Levee (Iberville Par.).

Univ. Nebraska State Mus., Manter L2b. Coll. No. 21199

Diagnosis (based on ten mature specimens): Body elongate, oval with a slight constriction between acetabulum and ovary, 1018 (820-1150) long by 563 (450-650) wide. Cuticle with small spines over anterior two thirds; posterior devoid of spination. Oral sucker unornamented, subterminal, 56 (46-66)long by 70 (55-79) wide. Prepharynx distinct, 13 (11-24) long. Pharynx 54 (50-57) long by 52 (48-55) wide. Esophagus long and slender, 123 (99-132) long. Ceca extend to caudal end of body. Acetabulum small, weakly defined,located in genital sinus posterior to genital openings, 41 (31-44) long by 41 (39-44) wide. Testes oblique, globular or ovoid; anterior testis 129 (99-154) long by 163 (99-187) wide; posterior testis 133 (110-165) long by 180 (150-224) wide. Vas efferens unite at level of ovary to form a conspicuous sigmoid seminal vesicle. Cirrus absent. Ovary ovoid, dextral to midline, 104 (99-115) long by 110 (99-125) wide. Seminal receptacle large, transversely oval, and lying directly posterior to ovary. Uterus makes 3-4 transverse, intercaecal loops before entering genital sinus. Vitellaria unite across body between the intestinal bifurcation and acetabulum, then extend laterally to posterior end of body. Vitelline ducts unite to form a vitelline reservoir between seminal vesicle and testes. Eggs 35 (33-37) long by 20 (17-22) wide. Excretory pore terminal; posterior stem of excretory vesicle sigmoid as it courses between the testes.

Discussion: *Apophallus venustus* has, heretofore, been reported from eastern coastal states and provinces of North America (Cameron, 1936; Babero and Shepperson, 1958; and Harkema and Miller, 1964). Yamaguti (1971) considers *A. venustus* conspecific with its European relative *A. donicus* (Skrjabin and Lindrop, 1919) Price, 1931, but we prefer to follow Cameron (loc. cit.) and recognize *A. venustus* as a distinct species based on its greater anterior extent of vitellaria and its larger size.

The life history of *A. venustus* was studied by Cameron (1937,a) and consists of an operculate snail, *Goniobasis livescens* (Menke), as first intermediate host, a wide variety of fishes as second intermediate host, and any fish-eating mammal as the definitive host. Cameron (1937,b) reported a human infection in Canada with *A. venustus* eggs being found in the feces. The epidemiology was traced to the presumed ingestion of fish.

The presence of *A. venustus* in Louisiana is of epidemiological interest since many of its people subsist, to a large degree, off the land. Small infections may perhaps go unnoticed because adequate diets prevent loss of vigor. However, Africa et al. (1935), working in the Philippines, found a high correlation between cardiac alteration and heterophyid infection. Kean and Breslau (1964) state that a large number of cardiac fatalities (14.6%) in the Philip-

pines are attributed to heterophyid eggs which find their way into the circulation. These reports, coupled with the already mentioned human infection with *A. venustus* should alert epidemiologists and pathologists to the presence of this speies and its possible involvement inhuman infection in Louisiana.

We found four of thirty raccoons infected with *A. venustus*. The infections were located throughout the small intestine and not localized only in the jejunum and ileum as reported by Cameron (1937,a).

Family OPISTHORCHIIDAE Braun, 1901

Parametorchis complexus (Stiles and Hassal, 1894) Skrjabin, 1913

(Figure 7)

Synonyms: *Ditoma complexum* Stiles and Hassal, 1894.

Hosts: *Procyon lotor* (Linn.).

Location: Biliary system.

Localities: Sherburne (Pointe Coupee Par.); 10 mi. S. of Ramah (Iberville Par.).

Univ. Nebraska State Mus., Manter Lab. Coll. No.

Diagnosis (based on ten mature specimens): Body flat, elongate, anterior end attenuate and posterior rounded, 7.8 (6.0-10.5) mm long by 2.2 (1.6-2.9) mm wide. Entire cuticle spinous; spines less dense posterior to testes. Oral sucker terminal, 272 (230-320) long by 326 (330-400) wide. No prepharynx. Pharynx muscular, 253 (210-290) long by 233 (220-270) wide. Esophagus short, 113 (70-150) long. Ceca large, coursing sinuously around organs until reaching posterior end of body. Acetabulum weak, inconspicuous, located in anterior one fourth of body, 286 (260-330) long by 305 (280-330) wide. Testes tandem, lobate, located in posterior half of body; anterior testis 913 (670-1250) long by 956 (800-1150) wide; posterior testis usually larger and possessing more lobes, 994 (800-1400) long by 955 (730-1200) wide. Vas deferens enlarged to form seminal vesicle that courses anteriorly, dorsal to uterus, and empties into genital pore. Genital pore located ventrally, midway between acetabulum and medially positioned vitellaria. Ovary trilobed, pretesticular, 405 (300-500) long by 494 (390-610) wide. Seminal receptacle variable in shape, usually larger than ovary, lying immediately posterior to, and often overlaping, the ovary. Uterus voluminous, with tightly packed loops loosely bordered by the ceca, occupying most of the space between ovary and acetabulum. Vitellaria laterally displaced in anterior half of body; unite medially betwen intestinal bifurcation and genital pore. Vitelline ducts unite ventral to ovary to form a vitelline reservoir. Eggs oval, some constricted anteriorly, 28 (26-30) long by 16 (15-17) wide. Excretory pore terminal; posterior stem of excretory vesicle sigmoid as it passes between testes, eventually giving rise to a Y-shaped excretory vesicle.

Discussion: Stiles and Hassal (1894) originally described *P. complexus* from specimens found inthe biliary system of cats in Maryland and New York. Since that time, additional species have been described from the biliary system of carnivores: *P. noveboracensis* Hung, 1926 from the cat; *P. intermedius* Price, 1929 from the fox, *Vulpes fulva* (Desmarest); *P. canadensis* Price, 1929 from *Mustela vison*; and *P. manitobensis* Allen and Wardle, 1934 from the dog. Cameron (1944) examined the morphology of these worms and concluded that the latter four species were synonyms of *Metorchis conjunctus* (Cobbold, 1860) Looss, 1899. He based his separation on the anterior disposition of the vitellaria. In *M. conjunctus* the vitellaria are laterally displaced while the genus *Parametorchis* is characterized by the anterior union of the vitellaria. Cameron's proposal left *Parametorchis* a monotypic genus. Yamaguti (1971) incorrectly stated that Cameron synonymized *P. intermedius, P. canadensis, P. noveboracensis,* and *P. manitobensis* with *P. complexus.*

Harkema and Miller (1964) reported *P. complexus* from one of 320 raccoons they examined in the southeastern United States (the infected raccoon was found in North Carolina). We have found *P. complexus* in five raccoons in Louisiana. The worms inhabit all levels of the biliary system One raccoon harbored 91 mature *P. complexus* and the bile duct exhibited marked hypertrophy.

SUMMARY

The following trematodes were collected from small mammals in southern Louisiana: *Alaria mustelae* Bosma, 1931; *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950; *Pharyngostomoides procyonis* Harkema, 1942; *Heterobilharzia americana* Price, 1929; *Apophallus venustus* (Ransom, 1920) Cameron, 1936; *Parametorchis complexus* (Stiles and Hassal, 1894) Skrjabin, 1913; *Baschkirovitrema incrassatum* (Diesing, 1850) Skrjabin, 1944; *Brachylaima virginianum* Dickerson, 1930; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961; *Hasstilesia texensis* Chandler, 1929; *Maritreminoides nettae* (Gower, 1938) Rankin, 1939; and *Rhopalias macracanthus* Chandler, 1932.

Trematodes reported from Louisiana for the first time are: *Alaria mustelae, Pharyngostomoides procyonis, Maritreminoides nettae, Baschkirovitrema incrassatum, Gyrosoma singulare, Apophallus venustus,* and *Parametorchis complexus.*

The raccoon is a new definitive host for *A. mustelae. A.mustelae* shows a distinct specificity for mustelids rather than procyonids based on larger size of worms, low number of naturally infected raccoons, and the low number of adults recovered from experimentally infected raccoons. During migration of larval *A. mustelae* in the raccoon, mesocerariae may lose their way and lodge in other tissues. The raccoon is, then, both a definitive and paratenic host. This finding becomes important in light of the recent report of *Alaria* mesocerariae in man in Louisiana (Beaver et al., 1977).

Pharyngostomoides procyonis is the most frequently encountered trematode in raccoons in Louisiana. Though it has been reported from the eastern coastal states and Texas, it likely is found throughout the other Gulf Coast states as well.

Metacercariae reported in crayfishes as *Maritrema obstipum* by Sogandares-Bernal (1965) are identical to adult *Maritreminoides nettae* recovered from raccoons, except for a protrusible cirrus and being ovigerous. The infected crayfishes are found in the same river basin as are the infected raccoons. We propose that they are the same species based on morphological, geographical and ecological criteria.

Specimens identified as *Baschkirovitrema incrassatum* have been reported in otters from North America, South America, and Africa. Since speciation in otters has ocurred, these worms possibly may be in the process of pursuing distinct evolutionary pathways. Our specimens from North America are much larger than previously reported and with no apparent overlap. Based on reported measurement, our specimens notably are more closely aligned with the material from South America than from Africa.

The presence of *A. venustus* in Louisiana is of epidemiological significance since a human infection involving this species has been previously reported. The metacercariae of *A. venustus* is foundin fish and all fish-eating mammals are susceptible, including humans. Since other heterophyids have been found in be the cause of cardiac fatalities, both epidemiologists and pathologists should be aware of its presence and the possible involvement in human infection in Louisiana.

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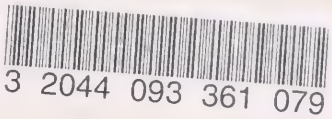
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